Hunting pressure and primate behaviour in the Gola forest of West Africa

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Abstract

Unsustainable hunting is leading to extensive overexploitation of wildlife. But how can we spatially quantify hunting in order to understand its impact on biodiversity? What effect is hunting pressure having on the behaviour of hunted species? And does behavioural change affect density estimates? This PhD project tackles these questions by focusing on hunted primates in the Gola forest of Liberia and Sierra Leone, West Africa.

Part of this project compares hunting pressure maps of the Gola region derived using different methods to assess potential differences in spatial outputs. The maps show considerable differences in hunting pressure distribution, suggesting that method chosen should be carefully aligned to the objectives of a study.

The central part of the PhD explores spatial variation in both baseline and reaction behaviours of Diana monkeys, *Cercopithecus diana*, and lesser spot-nosed monkeys, *Cercopithecus petaurista*, as a result of varying levels of hunting pressure. The different hunting maps were used as predictors to assess which measure best explains the variation in behaviour of these hunted species. I found that certain avoidance behaviours do change as a result of hunting and that some indicator maps of hunting pressure better predict behavioural change compared to others. These behavioural changes may have significant consequences for the fitness of the species and may decrease

detection probabilities, leading to biases in distance sampling methods for estimating population densities.

The final part of the PhD adopts an agent-based modelling approach to simulate the detection process of an observer conducting line transect surveys and incorporates observed changes in monkey behaviour to assess the potential indirect impact of hunting on density estimates. Results from the model give accurate estimates, highlighting this approach as a promising tool to model behavioural effects on density estimates in other species. Furthermore, results suggest that, at least when modelled separately, the recorded variation in behaviours linked to hunting does not affect density estimates of Diana monkeys and lesser spot-nosed monkeys.

In order to reverse negative population trends and establish sustainability thresholds, good population estimates and an accurate quantification of hunting are essential. Thus, mapping hunting pressure and quantifying the behavioural change associated with human predation is important to truly understand the indirect effect hunting may have on species.

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Chapter 1

Introduction

1.1 Hunting

Hunting practices have been carried out by humans for thousands of years, and the pursuit of wildlife as a resource was central to hunter-gatherer societies before the rise of agriculture and the domestication of animals (Panter-Brick et al. 2001). Despite current day societies relying primarily on domesticated livestock, in many tropical forests wildlife still represents a primary resource of food and income (Bennett and Robinson 2000). Hunting is thought to have caused vast wildlife extinctions in the past; the Holocene extinction of megafauna being the most notorious example of this (Turvey 2009). Nonetheless, if managed sustainably, hunting is not necessarily detrimental to wildlife, and carefully estimated sustainability indices have the potential to achieve a balanced equilibrium between human sustenance and the natural world (Sutherland 2001). Often however, a combination of factors results in a cumulative impact which is usually damaging to wildlife. Given the growing human population, the demand for resources worldwide has increased (Benítez-López et al. 2017). In many places, subsistence hunting is still vital for food and livelihoods, but it is increasingly being replaced by

commercial hunting and trade (Robinson and Redford 1994). The main drivers of wildlife harvest span from issues of food insecurity, to poverty and market dynamics to cultural preferences for hunted wildmeat (Abernethy et al. 2013; Brashares & Gaynor 2017). The social and political context may also greatly influence hunting dynamics, with governance and land management playing an important role in wildlife extraction patterns (Brashares and Gaynor 2017). Furthermore, improvements in road infrastructure aid accessibility to remote areas, and a widespread use of modern hunting technology increases the efficacy of hunting bouts significantly (Milner-Gulland et al. 2003; Benítez-López et al. 2017).

Inevitably, a combination of these factors results in unsustainable and detrimental effects on biodiversity (Fa et al. 2002; Milner-Gulland et al. 2003; Ripple et al. 2016), with an estimated 1.3 and 4.6 million tonnes of wildlife extracted in the Amazon and Congo basins respectively in 2010 (Nasi et al. 2011). “We must not let a forest full of trees fool us into believing all is well” (Redford 1992). Redford’s timely concept of “The Empty Forest” highlights the complexity of natural systems and the difficulty in quantifying the effects that anthropogenic pressures have on them. A seemingly biodiverse and intact forest may in fact have been deprived of the majority of its wildlife following exposure to human hunting pressure (Redford 1992; Harrison 2011).

The impacts of unregulated hunting are manifold. Aside from direct impacts on species numbers, hunting may cause non-lethal effects on hunted species, such as changes in behaviour induced by fear of humans (Brashares and

Gaynor 2017). Hunting does not only affect targeted species but has knock on effects on ecosystem function and forest dynamics: a reduction in seed predators and seed dispersals, for example, can have huge impacts on forest regeneration, a reduction in predators can cause shifts in prey densities and a reduction in prey species often results in reduced food for predators (Bennett and Robinson 2000). Furthermore, ongoing unsustainable extraction of wildlife will likely have devastating effects on the long-term sustenance of people who rely on wildmeat as a primary resource for subsistence (Ripple et al. 2016). If depletions continue at current high rates nothing will be left for future generations.

In order to recognise and prevent unregulated hunting it is important to measure spatial hunting patterns accurately. Furthermore, it is important to measure changes in density of animals as a result of hunting, since estimates of hunting sustainability are based on measured population trends over time and space and how these vary with hunting intensity (Robinson and Redford 1991). IUCN (International Union for Conservation of Nature) Red List categories rely on accurate density estimations to classify species threat categories and conservation measures vary accordingly (IUCN 2012). As mentioned above, species may change their behaviour as a result of hunting (Brashares and Gaynor 2017). This can make species less detectable and can potentially affect accurate estimations of their numbers. If a species' density is underestimated, it may be deemed unsustainably hunted and implemented conservation measures may consequently limit its harvest. This would render people that rely on wildlife for subsistence particularly vulnerable. It is

therefore important, both for wildlife and for humans, to accurately monitor hunting patterns and animal densities. But how can we spatially quantify hunting in order to understand its impact on biodiversity? What effect is hunting pressure having on the behaviour of hunted species? And does behavioural change affect density estimates? These questions are introduced in the following sections and explored in depth in the thesis chapters.

1.2 Hunting pressure indicators

An essential step in order to measure the effect of hunting pressure on wildlife is to understand spatial patterns of hunting itself. Without knowing the spatio-temporal distribution of hunting, in fact, how can we predict the effect it is having on species and ecosystems? As in many tropical areas hunting is a highly unregulated and remote process, it is extremely difficult to measure its spatial distribution (Peres et al. 2006). Methods used span from indirect indicators of hunting distribution, such as level of protection (Effiom et al. 2013; Rosin and Swamy 2013) and distance to human infrastructure (Yackulic et al. 2011; Constantino 2016), to more direct measures, such as distribution of hunting signs (Cronin et al. 2016; Trolliet et al. 2017) and recorded frequency of gunshots (Astaras et al. 2017; Prince et al. 2019). Although some methods are likely more informative than others and the spatial scales and effort required vary considerably between methods, a comparison and evaluation has not yet been realised. Such an evaluation may help to understand the suitability of different methods under different study objectives and may help improve predictions of the impact hunting has on

wildlife populations. In this thesis I will investigate differences in spatial distribution of hunting pressure resulting from multiple methods (Chapter 3).

1.3 Variation in risk and antipredator behaviour

The effects of anthropogenic predation on biodiversity have been widely documented across time and space, with studies focussing on the impact on numbers, community level effects and investigating trophic cascades and indirect effects on species composition and richness (Peres and Palacios 2007; Wang et al. 2007; Casini et al. 2008). Fewer studies (see the "Introduction" section of Chapters 4 and 5 for examples of these), however, focus on behavioural adaptations, often induced by hunting (Blumstein and Fernández-Juricic 2010).

Prey animals have developed a variety of adaptations to escape and defend themselves from predator attack. These can include morphological or physiological adaptations (i.e. spines, toxins) and behavioural antipredator strategies (Lima 1998; Kavaliers & Choleris 2001). Behavioural antipredator strategies can be grouped into baseline defences, adopted to minimise detection independently of predator presence, and reaction defences, carried out to increase the chances of survival once in the presence of a predator (Edmunds 1974). Many species alter their behaviour as a consequence of predation, for example by increasing their vigilance levels or by fleeing (Caro 2005). Behaviour, in fact, is a highly variable trait and it can be influenced in a plastic way following exposure to threat (Tuomainen and Candolin 2011).

Given the high fitness cost associated with behavioural change, since time is diverted away from activities such as foraging, resting and searching for mates (Amo et al. 2006; French et al. 2011), prey species are faced with constant optimisation trade-offs (Lima and Dill 1990). Both temporal and spatial variation in risk can shape the strength of behavioural adaptations of wildlife at different scales.

The Predation Risk Allocation Hypothesis (Lima and Bednekoff 1999) introduces the concept of time allocated to antipredator behaviours. In a theoretical framework, Lima and Bednekoff (1999) show that species will allocate more time to antipredator behaviours when the perceived risk of attack is high and more time to feeding behaviours when the perceived risk is low. For example, predator presence increases vigilance of 10 ungulate prey species in Zambia by a factor of 2.4, causing a 28% decrease in foraging behaviour (Creel et al. 2019). If, however, the risk of predation is sustained, species will decrease their antipredator response, since maintaining such response for prolonged periods becomes too costly (Lima and Bednekoff 1999). For example, convict cichlids, *Archocentrus nigrofasciatus*, exposed to prolonged background risk showed reduced responses to alarm cue concentrations compared to ones exposed to low levels of risk prior to the experiment (Brown et al. 2006). Antipredator responses therefore vary temporally in intensity according to the perceived level of risk encountered and the duration of that risk in time (Lima and Bednekoff 1999).

Predation risk may also vary spatially and Laundré et al. (2010) suggest that prey species form a mental map, termed the "landscape of fear", based on perceived spatial variation in risk. Female elk populations, *Cervus elaphus*, in Yellowstone National Park, for example, increased their vigilance levels (Laundré et al. 2001) and used sub-optimal habitats (Creel and Winnie 2005) after wolves were reintroduced between 1994-1995. Thus, in areas where wolves were reintroduced and the perception of risk was greater, elk antipredator behaviour changed significantly. Prey animals are thus constantly making decisions shaped by a landscape of fear and temporal variation in risk to ultimately increase fitness-enhancing activities (Frid and Dill 2002).

Many factors may alter the antipredator response adopted by a species. This may depend on personality (Quinn and Cresswell 2005), may be context-dependent or predator-dependent (Caro 2005). Species can modify antipredator behaviours according to the predator; with responses varying, for example, according to the predator hunting strategy or whether it is an aerial or a terrestrial predator (Caro 2005). Ambush predators such as leopards for example, tend to elicit a response in their prey that signals detection to the predator, whereas pursuit predators such as chimpanzees and humans, are likely to cause an increase in avoidance behaviours in prey species (Caro 2005). When exposed to carnivore, snake and raptor models, grey mouse lemurs, *Microcebus murinus,* observed and monitored the carnivore and snake models but exhibited cryptic and freezing behaviour when exposed to a raptor model (Rahlfs and Fichtel 2010). Given the pursuit nature of the

human hunting strategy and the modernization of hunting practices, there is likely an increased pressure for antipredator behaviours to minimise detection against human predators (Lima 1998; Fa and Brown 2009). When predation has a strong negative effect on fitness, spatio-temporal variation in risk can strongly drive wildlife dynamics.

The lack of studies on an animal's response to hunting are partly linked to the difficulty in identifying the direct impacts of behavioural change on population persistence and the consequent conservation implications these changes may have (Anthony and Blumstein 2000). Furthermore, it is often difficult to collect behavioural data on hunted species, since these likely occur at low densities and are avoidant of humans (Fa and Brown 2009). Quantifying the effect that hunting pressure may have on the behaviour of hunted species is important, since it can highlight potential non-lethal consequences of human predation and can help understand the potential impact on the detectability of these species. Variation in antipredator adaptations to minimise conspicuousness, resulting from spatio-temporal variation in risk perception, may indeed lead to variation in detectability which in turn may affect density estimates in regions with varying human predatory pressures. This thesis tries to understand the interactions between hunting and behavioural change by focussing on the behaviour of two West-African monkeys, and how it may vary as a result of hunting pressure (Chapter 4 & 5)

1.4 Detectability and density estimates

One of the main methods used to estimate population densities is distance sampling (Buckland et al. 2001). Using the perpendicular or radial distances between transect lines (or points) and study objects, this method estimates the proportion of animals detected in the surveyed area. Given the distribution of perpendicular distances, a fitted detection curve then estimates the proportion of animals missed and consequently extrapolates a density estimate for the whole region (Buckland et al. 2001). Two of the key distance sampling assumptions are that 1. all individuals on the line or point are detected, and 2. individuals do not move in response to surveyors prior to being detected (Thomas et al. 2010). Changes in behaviour as a result of human hunting pressure, however, may lead to reduced detection on the line and detections of animals away from their initial location (Table 1.1) which, if not accounted for, may result in a bias in census results when estimating population densities.

Few studies have looked at the implications of spatio-temporal behavioural shifts on detection probabilities (Johns 1985; Nijman 2007; Robertson et al. 2016). Robertson et al. (2016) modelled the impact of altered diving behaviour induced by seismic operations on density estimates of bowhead whales, *Balaena mysticetus,* from aerial surveys. Results suggest that numbers were underestimated when behavioural change was not accounted for. Similarly, the densities of rainforest Galliformes were underestimated by 13-20% during periods of reduced vocalisation (Nijman 2007).

Given the increased likelihood of avoidance behaviours under high hunting pressure, a reduction in detectability due to antipredator behavioural change may lead to underestimates of population densities in areas under higher risk of predation. Some examples of the predicted effects of previously recorded changes in behaviour due to hunting on detectability and density estimates are summarised in Table 1.1. No research has yet quantified the effect of change in detectability resulting from shifts in antipredator responses under a known level of human predation risk. Understanding how this change may affect density estimates, however, becomes an important step when trying to quantify the indirect effect that hunting may have on species' numbers. This thesis uses an agent-based modelling approach to quantify the impact of behavioural variation due to hunting on detectability and density estimates (Chapter 6).

Table 1.1 Examples of potential effects that antipredator behavioural shifts due to hunting pressure (Source studies in parenthesis) may have on detectability, distance sampling assumptions (1. Objects on the line or point are detected with certainty, 2. Objects do not move; Thomas et al. 2010) and consequently on density estimates

Behaviour	Type of change	Prediction	Potential effect on distance sampling assumptions	Density estimate bias
Vocalisation and mobbing	Decrease (Bshary 2001; Hicks et al. 2013)	Decreased detectability - less likely to detect individuals that do not sound alarm calls or attack	Less vocal, may bias assumption of certain detection on the line. Also, if using mean cue rate from other sources to estimate density this may bias census results	**Underestimating** density in hunted regions
Grouping	Decrease (Watanabe 1981; Dooley and Judge 2015)	Decreased detectability - less likely to detect individuals that live in smaller groups	Less conspicuous, may bias assumption of certain detection on the line. Also, if using group size data from other sources to estimate density this may bias census results	**Underestimating** density in hunted regions
Freezing	Increase (Kümpel et al. 2008)	Decreased detectability - less likely to detect individuals that freeze to avoid exposure	Less conspicuous, may bias assumption of certain detection on the line	**Underestimating** density in hunted regions
Fleeing	Increase (Croes et al. 2006; Magige et al. 2009; Muposhi et al. 2016; Smith et al. 2017)	Decreased detectability - less likely to detect individuals that escape at a greater distance	Fleeing may bias assumption that animals do not move prior to detection by the observer. If animals remain in range bias likely to be low. If animals move beyond range this will lead to greater bias in census results	**Underestimating** density in hunted regions
Vigilance	Increase (Ciuti et al. 2012; Tarjuelo et al. 2015)	Decreased detectability - less likely to detect individuals that are more wary and likely to detect humans first	Greater vigilance may lead to responsive movement and therefore may bias assumption that animals do not move prior to detection by the observer	**Underestimating** density in hunted regions
Activity pattern	Shift in activity away from hunting periods – i.e. increased nocturnality (Ohashi et al. 2013, Marchand et al. 2014)	Decreased detectability – if hunting periods coincide with survey periods: less likely to detect individuals that reduce activity during those times	Sleeping or less active, may bias assumption of certain detection on the line.	**Underestimating** density in hunted regions

1.5 Primates and West Africa

To address the above gaps in the literature, this thesis uses primates as a model species. Non-human primates (referred to hereafter as primates) are highly vulnerable to anthropogenic disturbances (Kalbitzer and Chapman 2018). Given their slow life histories and because they tend to occur at relatively low densities (Cowlishaw and Dunbar 2000), primates strongly suffer the consequences of a human dominated world (Kalbitzer and Chapman 2018). A recent study has estimated that around 60% of primate species are now threatened with extinction and around 75% have declining populations due to increasing pressures driven by increased demand for resources (Estrada et al. 2017). Amongst threats such as loss of habitat due to agricultural expansion, logging and livestock farming, hunting and trade were recognized as important drivers of this trend (Estrada et al. 2017). From China, through to Indonesia, Liberia and Brazil, species such as the western black-crested gibbon, the Hose's leaf monkey, the upper guinea red colobus and the buff-headed capuchin all suffer the consequences of anthropogenic hunting pressure (Bleisch et al. 2008; Nijman et al. 2008; Kierulff et al. 2015; Oates et al. 2016). The need to understand human-primate interactions and the ecology and behaviour of many primate species has been identified as an urgent research priority (Estrada et al. 2017).

As a study site this thesis focusses on the tropical forest of West Africa. Wildmeat hunting is a strong driver of defaunation trends in West and Central Africa (Abernethy et al. 2013; Petrozzi et al. 2016). In tropical Africa,

wildmeat represents a central source of animal protein and in rural communities it is often essential for food security and financial stability (Wilkie et al. 2005, 2016). Communities surrounding tropical forest habitats rely more on wildmeat compared to those surrounding savannah regions since livestock farming is limited by the forest habitat type (Wilkie et al. 2016). The demand for wildmeat in many West and Central African countries is high and as a trade it is often reported to be only second to agriculture as an income source (Petrozzi et al. 2016). In Liberia and Sierra Leone, hunting is causing wildlife declines, including declines in primate species (Tweh et al. 2014). Increasing demands for wildmeat have led to the exploitation of different primate species to unsustainable levels (Junker et al. 2012). Compared to other African countries, however, limited data on patterns of wildmeat consumption and their consequence for wildlife is available for these countries (Taylor et al. 2015).

1.6 Summary of research questions

The main aim of this thesis is to explore variation in primate antipredator behaviours as a result of varying levels of hunting pressure in the Gola forest of Liberia and Sierra Leone, and to understand how this may influence detectability and density estimates of primate populations. This will be achieved through the following research questions:

1. What are the main commonalities and what the key differences between maps of hunting pressure built using different methods? (Chapter 3)

2. What is the effect of hunting pressure on the antipredator behaviours of hunted species? (Chapter 4 & 5)

3. How does behavioural change linked to hunting pressure impact the density estimates of hunted species? (Chapter 6)

1.7 Thesis outline

Chapter two is a methods chapter that describes the study site, including information on local culture, climate and biodiversity. It also provides a description of the study species and details of field data collection and analysis techniques. The chapter ends with a reflection on the fieldwork experience.

Chapter three investigates different methods for estimating spatial variation in hunting pressure and highlights commonalities and differences between them.

Chapter four explores differences in baseline antipredator behaviours (adopted irrespective of predator presence) of Diana monkeys, *Cercopithecus*

diana, and lesser spot-nosed monkeys, *Cercopithecus petaurista*, as a result of the different estimates of hunting pressure distribution investigated in chapter three.

Chapter five explores differences in reaction antipredator behaviours (adopted as a reaction to predator presence) of Diana monkeys, *Cercopithecus diana*, and lesser spot-nosed monkeys, *Cercopithecus petaurista*, as a result of the different estimates of hunting pressure distribution investigated in chapter three.

Chapter six investigates the potential effect of behavioural change due to hunting recorded in chapter five, on density estimates of Diana monkeys and lesser spot-nosed monkeys through an agent-based modelling approach**.**

Chapter seven summarises the results of the thesis as a whole, integrating aspects from all chapters and highlighting the importance and implications of these in a broader context.

Chapter 2

Methods

2.1 Study Site

2.1.1 Location

To explore the relationship between hunting pressure and primate behaviour, fieldwork was conducted in the Gola region, part of the Upper Guinean Forest (Figure 2.1), on the border between Liberia and Sierra Leone in West Africa (Figure 2.2).

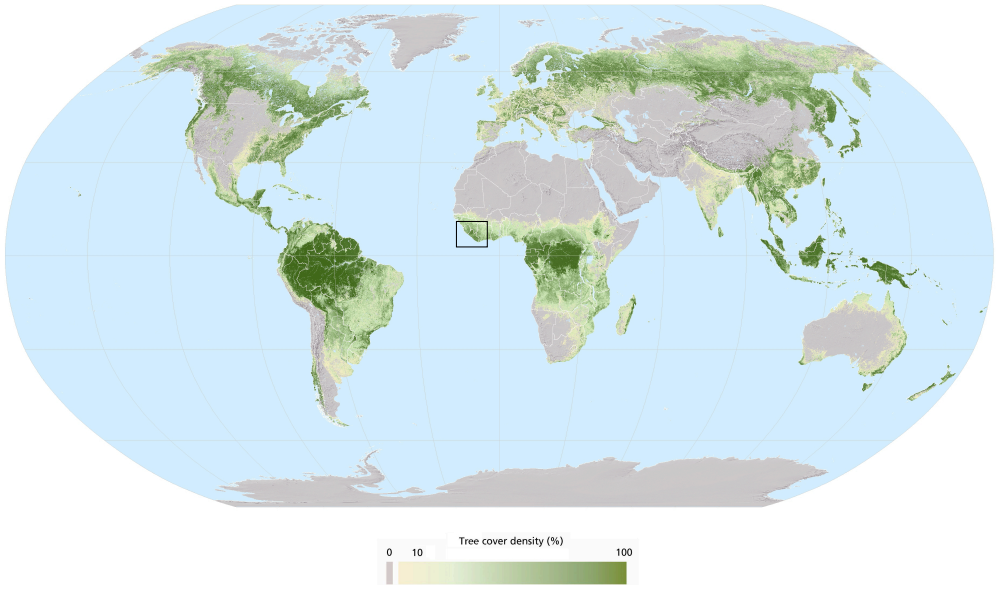

Figure 2.1 World tree cover density (%) in 2010. Area in box corresponds to the Upper Guinean Forest of West Africa (Source: Food and Agriculture Organization of the United Nations (FAO))

This study site is home to many primate species and spans across areas with different degrees of law enforcement, likely creating a gradient in hunting pressure essential to the proposed study. Furthermore, an existing set of transect lines across the area meant fewer lines were cut for the purpose of this project, thus reducing the physical impact of the study. This region was primarily chosen due to existing contacts established in both countries by Sorrel Jones, a member of the Conservation and Behaviour lab group who has spent extensive time working in Gola, Liberia. Sorrel helped to build relationships with people in both Liberia and Sierra Leone who were able to answer questions about the site prior to fieldwork and were instrumental in the successful completion of the study. A pilot study of two months, conducted between May and June 2017 in Liberia, further helped consolidate and strengthen contacts with local counterparts and test field methodologies.

The Upper Guinean forest is considered one of the 25 most biodiversity rich hotspots in the world (Myers et al. 2000) and Gola is one of the last intact areas of dense moist evergreen and semi-deciduous forest remaining in the Upper Guinean forest. As one of the last fragments of this habitat in the region and due to its richness in endemic biodiversity, the area is of considerable conservation concern (Hillers 2013) and should thus receive significant research attention.

The study region can be broadly categorised into three distinct areas (Figure 2.2, Figure 3.2). The Gola Rainforest National Park (GRNP) of Sierra Leone (7°61'N, 10°94'W) covers an area of 700 km^2 and was inaugurated in 2011.

The park has established on-the-ground law enforcement in the form of regular ranger patrols deployed throughout the park, covering around 7000 km per year (Barca et al. 2018b). The effectiveness of the park's conservation interventions is highlighted by positive figures showing increasing populations of the Endangered Upper Guinea red colobus, *Piliocolobus badius*, for example (Barca et al. 2018a). This suggests an effective reduction in hunting pressure since the establishment of the park.

In contrast, the Gola Forest National Park (GFNP) of Liberia (7°47'N, 10°82'W) covers an area of around 980 km^2 and was demarcated in early 2018, at the time of data collection. When the hunting data was collected for this study, park regulations to prevent hunting activities were thus less established than in the GRNP. A lack of strong patrol effort and the new establishment of park boundaries means hunting pressure in this region is likely relatively high compared to the neighbouring GRNP. Earlier evidence does in fact support higher overall hunting pressure in the GFNP compared to the GRNP (Hillers 2013; Lahai 2013).

The third area is a community forest adjacent to the GFNP in Liberia (7°74'N, 10°52'W) and covers about 400 km^2. Through a partnership between the communities, the Government of Liberia and conservation NGOs (the Society for Conservation of Nature in Liberia, SCNL, and the Royal Society for the Protection of Birds, RSPB), the GolaMA project (running between 2014 and 2019) has been working to implement and establish this community forest, with the aim of achieving sustainable management of forest resources

outside protected areas (Jones et al. 2018). For simplicity this area will be referred to as the community forest hereafter. Work by Jones et al. (2018) indicates that, similarly to the GFNP, hunting in the community forest is widespread.

Different gun regulations between countries, with stricter rules in Sierra Leone compared to Liberia, may also translate into different degrees of hunting pressure between areas (Lahai 2013). Therefore, overall differences in both local management and country level legislations likely result in different patterns of biodiversity exploitation and degree of hunting pressure across the Gola forest region, with the lowest hunting pressure expected in the GRNP of Sierra Leone and higher hunting pressure expected in both the GFNP and the community forest of Liberia.

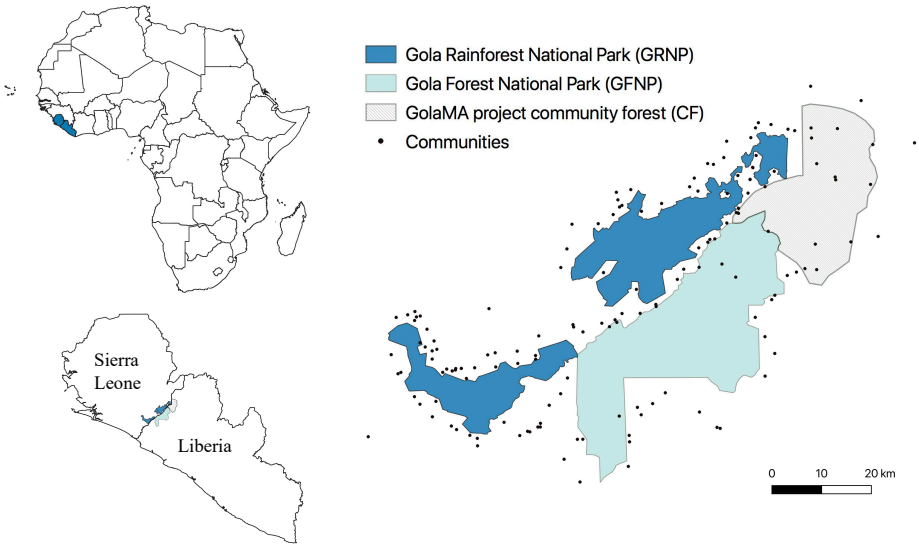

Figure 2.2 Location of the study: the Gola forest region of Liberia and Sierra Leone. Community forest: GolaMA project community management area (Liberia), GFNP: Gola Forest National Park (Liberia), GRNP: Gola Rainforest National Park (Sierra Leone**)**

2.1.2 Ethnicity and livelihoods

In Liberia, the Gola forest lies primarily within the Kongba District, Gbarpolu County. On the Liberian side the site has relatively low population density; migration to the region for mining, logging and hunting practices has resulted in a population of very diverse people originating from ethnically diverse backgrounds (Jones et al. 2018). Within the GolaMA project area, 65% of the population belong to either the Gola, Mende or Kissi tribe (Jones et al. 2018). In Sierra Leone, the GRNP lies between the Kailahun, Kenema and Pujehun districts, within the Eastern Province. Around the GRNP in Sierra Leone the majority of the population (86%) identifies as part of the Mende tribe, with only 6.3% identifying as Gola (Bulte et al. 2013).

Across the region, literacy levels are very low, with only 29% of the adult population being able to read or write across the forest edge communities in Sierra Leone, for example (Bulte et al. 2013). This is primarily due to lasting devastating effects of the relatively recent civil wars that occurred in both countries, with most communities suffering from severe poverty and lacking good road infrastructure as well as educational facilities and basic health services (Bulte et al. 2013). In both countries subsistence agriculture is the primary livelihood strategy, alongside the cultivation of commercial crops such as oil-palm, cocoa and coffee (Jones et al. 2019). Around the GRNP in Sierra Leone, agricultural production provides the main source (90%) of income, with rice cultivation as the primary farming activity (Bulte et al. 2013). Similarly in Liberia, around 98% of households practiced agriculture

(Jones et al. 2018). Other major livelihood strategies include small-scale mining, reflecting the area's deposits of gold and diamonds, selective logging and trading of timber, and gathering of non-timber forest products (Bulte et al. 2013). On the Liberian side, hunting is practiced by about 40% of households (Jones et al. 2019). The commercialisation of wildmeat hunting provides a strong source of income with hunters reporting higher incomes from wildmeat sales compared to other livelihood strategies (Jones et al. 2019). 85% of harvested biomass of the catch hunted in the GolaMA project region, for instance, was sold to traders (Jones et al. 2019).

2.1.3 Climate and geology

Gola lies in the wet tropical climatic zone and is thus subject to high levels of precipitation (Tubbs 2015). The average yearly rainfall is usually between 2500-3000 mm, with substantial monthly variation (Figure 2.3) (Klop et al. 2008).

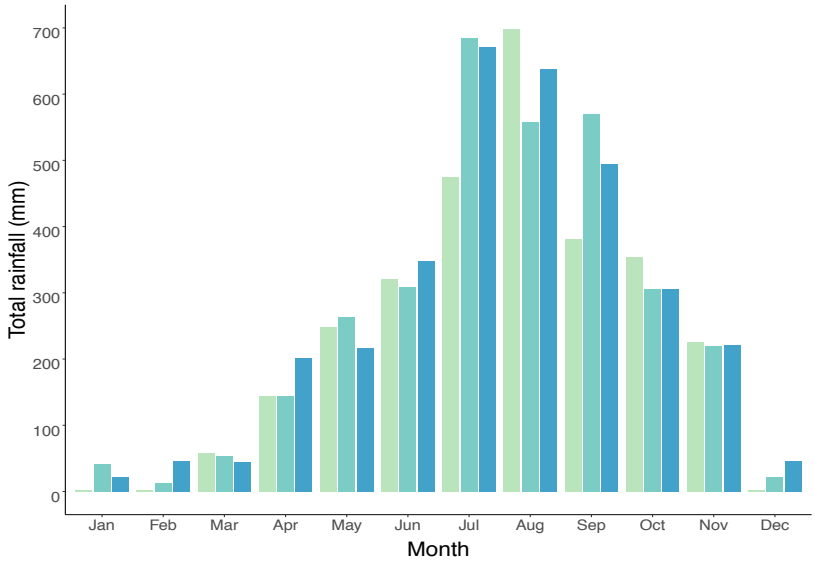

Figure 2.3 Total annual rainfall measured at three sites (Wayehun, Sileti, and Nemahungoima) around the GRNP in Sierra Leone in 2007 (Source: data extracted from graph in Klop et al. 2008)

Highest precipitation occurs during the months of July and August (up to 700 mm per month), whereas the period from December to March is considered the dry season, with minimal rainfall occurring during this time (less than 50 mm per month). In 2007, mean annual precipitation measured at three sites (Wayehun, Sileti, and Nemahungoima) within the GRNP in Sierra Leone was 3117 mm, higher than previously recorded averages (Klop et al. 2008) (Figure 2.3). Temperatures oscillate around 27 °C, with higher averages in March and lower averages in August (Davies 1987). Humidity remains high year-round. The region is characterised by many small water courses and a few major rivers. The Moro and Mano rivers form a natural border between Liberia and Sierra Leone (Tubbs 2015). Altitude ranges from around 100 to 430 metres (Tubbs 2015). The Gola region is formed of ancient crystalline rocks that date to the Precambrian period and substrates are characterised mainly by soils derived from granite (Wilson 1965).

2.1.4 Vegetation and biodiversity

Gola is primarily classified as a moist evergreen and semi-deciduous forest (Figure 2.4), however freshwater inland swamp forest, farm bush, herbaceous swamp and large areas of secondary forest (as a result of historical intensive logging) can also be found in the region (Klop et al. 2008). The Gola region is home to a huge number of endangered and threatened species. Over 2800 species (650 endemic) of vascular plants have been recorded across the Upper Guinean forests (Jongkind 2004). Of these, 899 species have been recorded in the GRNP, Sierra Leone (Klop et al. 2008). Over 600 species of butterfly

have been documented in the GRNP, as well as 43 species of amphibian and 13 of reptile (Gola Rainforest National Park (GRNP) website - https://golarainforest.org/wildlife). Many endemic and threatened bird species can also be found in Gola, amongst these some flagship species such as the white-necked rockfowl, *Picathartes gymnocephalus* (symbol of the GRNP), and the elusive Gola malimbe, *Malimbus ballmanni*. The rich biodiversity includes 49 species of large mammals, of which 9 are threatened. Amongst these the pygmy hippopotamus, *Choeropsis liberiensis*, the forest elephant, *Loxodonta africana cyclotis*, Jentink's duiker, *Cephalophus jentinki*, and 10 species of primate (Klop et al. 2008).

Figure 2.4 Examples of the Gola forest habitat from above and below the forest canopy (photos by Camilla Blasi Foglietti)

2.2 Study Species

The 10 primate species recorded in Gola include two prosimians, seven monkeys and one ape (Table 2.1). These species are subject to differing levels of vulnerability to anthropogenic pressure, dependant on activity patterns, behaviour, ecological requirements and human hunting preference (McGraw et al. 2007). Species with small geographic ranges and narrow ecological niches, such as the Diana monkey and the Upper Guinea red colobus monkey for example, are particularly susceptible to habitat loss (Oates 2011). The major threat for many of these species, however, is hunting. The main primate species affected by hunting are those with a large body size, those that are restricted to high canopy strata and that live in large and vocal social groups (Oates 2011). These are easier for hunters to detect and deliver a better reward per unit of hunting effort (Refisch and Koné 2005).

For this study, data on the following diurnal primates was recorded: Diana monkey (*Cercopithecus diana*), lesser spot-nosed monkey (*Cercopithecus petaurista*), Campbell's monkey (*Cercopithecus campbelli*), sooty mangabey (*Cercocebus atys*), and Upper Guinea red colobus monkey (*Piliocolobus badius*) (Figure 2.5). These species were chosen based on encounter rates during a pilot study and based on differences in vulnerability to hunting (i.e. variation in body size, habitat sensitivity, density and group size). Of these five species, the most frequently encountered during the core data collection period were Diana monkeys and lesser spot-nosed monkeys (Figure 2.5), thus these species are the main focus of this thesis. The samples size for the other

species was not large enough for robust statistical analysis. For those species simple descriptive statistics are presented in Appendix 3.

Table 2.1 List of primate species of the Gola region with associated threat status. EN: Endangered; VU: Vulnerable; NT: Near Threatened; LC: Least Concern (Drawings by Camilla Blasi Foglietti)

Common name	Latin name	Conservation status (date of assessment)	
Diana monkey	*Cercopithecus diana*	EN (2019)	
Lesser spot-nosed monkey	*Cercopithecus petaurista*	LC (2008)	
Campbell's monkey	*Cercopithecus campbelli*	LC (2008)	
Sooty mangabey	*Cercocebus atys*	NT (2008)	
Western black and white colobus	*Colobus polykomos*	VU (2008)	
Upper Guinea red colobus	*Piliocolobus badius*	EN (2020)	
Olive colobus	*Procolobus verus*	VU (2018)	
Chimpanzee	*Pan troglodytes*	EN (2016)	
West African potto	*Perodicticus potto*	LC (2008)	
Demidoff's Galago	*Galagoides demidoff*	LC (2016)	

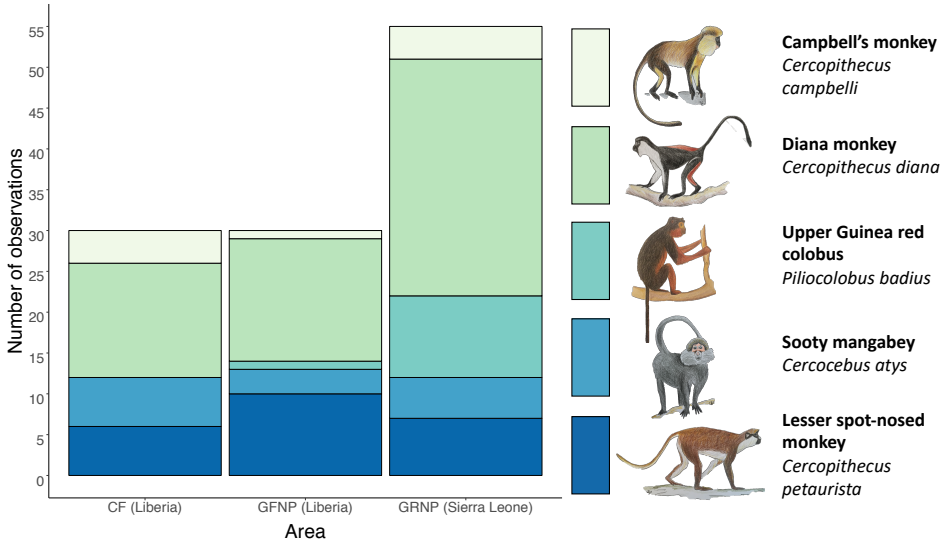

Figure 2.5 Number of visual observations for each species in the community forest (CF): Campbell's monkey = 4, Diana monkey = 14, red colobus = 0, sooty mangabey = 6, lesser spot-nosed monkey = 6; the Gola Forest National Park (GFNP): Campbell's monkey = 1, Diana monkey = 15, red colobus = 1, sooty mangabey = 3, lesser spot-nosed monkey = 10; and the Gola Rainforest National Park (GRNP): Campbell's monkey = 4, Diana monkey = 29, red colobus = 10, sooty mangabey = 5, lesser spot-nosed monkey = 7 (Drawings by Camilla Blasi Foglietti)

2.2.1 Diana monkey

Diana monkeys, *Cercopithecus diana*, are medium-sized, arboreal monkeys with a geographic range that extends from Guinea to Côte d'Ivoire (Figure 2.6). They are restricted to high forest canopy and are highly susceptible to habitat modification (Oates et al. 1990; McGraw et al. 2007), living mainly in undisturbed forest. They weigh between 3.5 and 5 kg and their home range is between 0.5 to 1 km^2 (McGraw et al. 2007). Diana monkeys spend between 40-45% of their time feeding and foraging and about 25% moving, although these numbers vary considerably between groups and years (Oates 2011), and presumably with perceived threat levels. Diana monkeys are a very vocal species, with an elaborate repertoire of contact calls and alarm calls (Figure 2.8) specific to different predators (Zuberbühler et al. 1997).

They live in large social groups of 15-30 individuals with one adult male and several adult females, subadults and juveniles (Oates 2011). Diana monkeys are primarily frugivorous, but also feed on leaves and insects depending on time of year and resource availability (Buzzard 2006). They often occur in polyspecific groups, particularly in association with red colobus and followed by lesser spot-nosed and Campbell's monkeys (Bshary and Noë 1997a). The main predators of Diana monkeys are leopards, eagles, chimpanzees and humans (Bshary and Noë 1997a), although humans exert the strongest predatory pressure on this species by far (Oates 2011). The species is listed as Endangered on the IUCN Red List of Threatened Species. As Diana monkeys rely on primary forest, which has been considerably cut down across West Africa (through selective logging, mining and agricultural expansion), and given their relatively large body size and their occurrence in large, highly vocal groups, this species is considerably more vulnerable to hunting pressure compared to other guenons (Oates 2011).

Figure 2.6 Geographic range of Diana monkey and lesser-spot nosed monkey. Diana monkey geographic range is smaller and entirely overlaps the geographic range of lesser spot-nosed monkey (Source: IUCN Red List of Threatened Species, (Oates et al. 2008; Koné et al. 2019))

2.2.2 Lesser spot-nosed monkey

Lesser spot-nosed monkeys, *Cercopithecus petaurista*, are smaller arboreal monkeys with a relatively large geographic range that extends from Guinea Bissau to Togo (Figure 2.6). They survive well in disturbed habitats and are often found near agricultural land and villages, as well as in secondary forest (Oates 2011). Lesser spot-nosed monkeys rarely use the top forest strata and spend most of their time in the forest understory (McGraw 2000). They weigh between 2.9 and 4.4 kg and their home range is between 0.5 to 0.8 km^2 (Oates et al. 1990; McGraw et al. 2007). They have been reported to spend around 45% of their time feeding and foraging, 26% of time moving and 24% of time resting (Oates 2011). Estimated average group size is around 14 individuals (Oates et al. 1990). Again, groups normally contain a single male alongside adult females, subadults and juveniles. Lesser spot-nosed monkeys have been found to feed primarily on leaves, followed by fruit (Buzzard 2006). This species also lives in close association with other species, primarily with Diana monkeys and Campbell's monkeys (Buzzard 2010). This species is extremely cryptic as compared to Diana monkeys: lacking highly visible coat markings, living in smaller groups, vocalising with softer contact calls and moving stealthily. Despite its cryptic behaviour, lesser spot-nosed monkeys are still predated upon, especially by humans. The species is listed as Least Concern on the IUCN Red List of Threatened Species. Given its small size and cryptic behaviour it is not a preferred catch by hunters; furthermore, their adaptability to use disturbed habitats makes them more resilient (Oates 2011). However, declining numbers of other hunted monkeys make them an increasing target.

Indeed a study across the community forest in Gola found that lesser spot-nosed monkeys comprised 3.2% of the carcasses hunted, where Diana monkeys comprised 2.7% (Jones et al. 2019).

2.3 Data collection

2.3.1 Hunting pressure maps

Different hunting maps were generated to assess the comparability of different methods used to estimate hunting pressure and in order to predict change in monkey behaviour associated with hunting. The methodology for generating the hunting maps as well as further details on data collection of hunting measures are given in Chapter 3. The methods are briefly outlined below:

2.3.1.1 Distance from human settlements

This method estimates the level of hunting pressure of a specific area based on distance from the closest human settlement. All villages and towns were mapped as point features weighted by human population size. An impact radius was then calculated using kernel density estimators based on data on maximum distance travelled by hunters in Gola.

2.3.1.2 Encounter rate of hunting signs

This method estimates the distribution of hunting based on encounter rate of hunting signs (i.e. gun shells, snares) collected along transect lines (Figure

2.7 a) distributed throughout the study region. The map is built using inverse distance weighted interpolation with the centre of each transect as a point feature and encounter rate as an assigned value.

2.3.1.3 Gunshot frequency

This method estimates hunting pressure distribution based on frequency of gunshots recorded by Audiomoth recording devices (Hill et al. 2018) placed across the study region (Figure 2.7 a). The map is built using inverse distance weighted interpolation with the location of each device as a point feature and the frequency of recorded gunshots as an assigned value.

2.3.1.4 Law enforcement area

This indicator is based solely on legislative differences in degree of law enforcement. Within the Gola region, three areas with differing levels of law enforcement were identified: the GRNP in Sierra Leone, the newly established GFNP in Liberia and its adjacent community forest, which has reduced hunting regulations.

2.3.2 Primate behavioural observations

Behavioural observations were conducted between October 2017 and May 2018. In Sierra Leone data was collected between October and November 2017 and between January and March 2018, in Liberia data was collected between November and December 2017 and between March and May 2018. Alternating between countries helped to account for potential variation linked

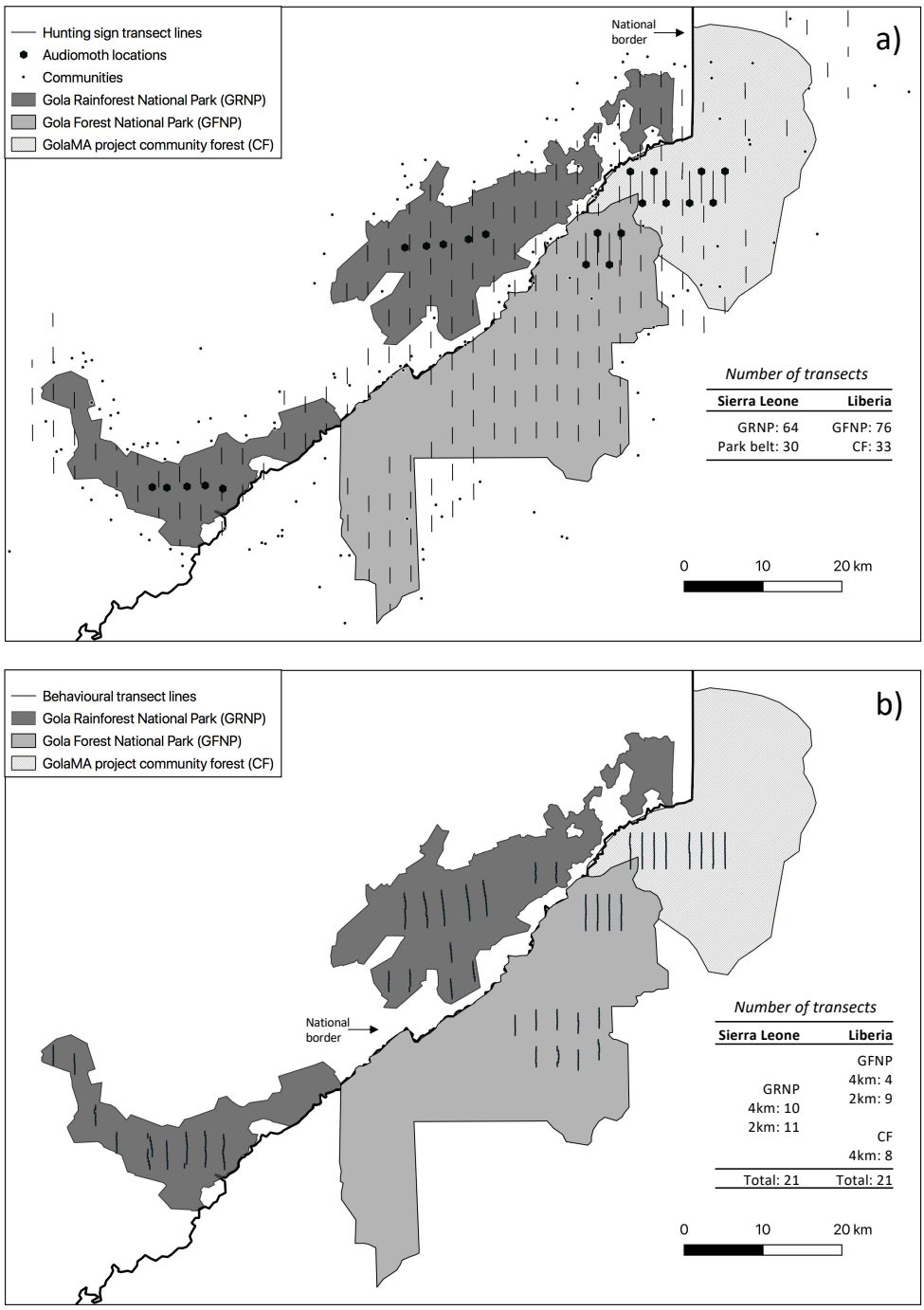

Figure 2.7 Location and number of transect lines **a)** surveyed to collect hunting sign data (collated across 3 datasets collected between 2011 and 2018) and **b)** surveyed between October 2017 and May 2018 to collect the behavioural data central to this study. Map **a)** also shows the location of Audiomoth recording devices used to collect gunshot frequency data and the location of communities

to time of year. A total of 22 permanent 4-km transects were monitored (10 in the GRNP, 8 in the community forest and 4 in the GFNP). These lines are normally used as part of the ongoing monitoring in both countries. Additionally, 20 2-km lines were cut specifically for this study at least 2 weeks prior to the data collection phase (11 in the GRNP and 9 in the GFNP). The 2-km transects and the permanent transects in Sierra Leone were spaced at a distance of 2.5 km, whereas the permanent transects in Liberia were spaced at a distance of 1.5 km (Figure 2.7 b). All transects were sampled once, with the exception of 3 lines in Liberia, which were sampled a second time as no successful observations were recorded during the first attempt. Total survey effort was thus 134 km across the survey region, with 62 km walked in the GRNP, 32 km walked in the community forest and 40 km walked in the GFNP. Transects were only walked once to ensure true independence of each observation. Observations on different transect lines are expected to be independent as the home rages of the focus species are smaller than the distance between transect lines.

Observations started in the morning, between 6:45 am and 7:30 am. Each day a 2-km transect was monitored. The 4-km transects were split into 2 and monitored on 2 consecutive days. Survey teams varied between 2-4 people, with CBF present during all observations. Observers walked transects at a slow pace (0.5-1km/h), scanning the surroundings with the use of binoculars and listening for monkey calls. Transects were walked in silence to minimise the chance of being detected by monkey groups/individuals. If monkeys were located through vocalisation, the observers left the transect line (up to a

maximum of 500 m) towards the direction of the calls and returned to the same point along the transect to continue the survey once the observation was completed.

Upon detection of a primate group (through sight or vocalisation), the experimental phase would begin. The observers remained hidden out of view for a period of 5 minutes (or until detected) to gather baseline group-level information on primate behaviour prior to detection. Species, number of individuals within the group, group cohesion and presence of other species was recorded (Table 2.2). The visibility of groups/individuals was assessed by counting the number of visible body parts through 2 group scans (unless observers were detected), with a 1-minute interval in between (Table 2.2). This was repeated following detection in order to get a measure of change in visibility. Following detection, however, it was not always possible to get 2 group scans, as often the monkeys would flee before the 1-minute interval. Height of monkeys prior to detection was estimated by assigning each visible monkey to a height category (Table 2.2). Presence/absence of movement and freezing behaviours was also recorded.

If the observers had not been detected at the end of the 5-minute period, the observer walked towards the group and recorded the distance at which the primate group detected the observer as the reaction distance (Table 2.2). Detection by the monkey groups was identifiable as it usually resulted in a sudden change in behaviour which could include any of the following: individuals started to vocalise or changed type of call, individuals started

inspecting, individuals stopped feeding or grooming, individuals increased their movement behaviour or fled abruptly. Following detection, the reaction of the group/individual was scored as one of six categories (Table 2.2) (Croes et al. 2006; Koné and Refisch 2007). A handheld recorder was used to continuously record vocalisations for both prior and post detection periods. Following detection, the group was observed for up to a maximum of 20 minutes, providing the group did not flee. Following this period, the observer approached the group further and recorded flight initiation distance (FID) of the closest individual (Table 2.2). GPS coordinates for the estimated centre of each group were then recorded. The observers then continued walking the transect until the next group was detected. All transects were surveyed following this procedure.

All GPS coordinates were collected using a Garmin GPSMAP 64s handheld navigator. Time was kept using a Casio F-91W wristwatch and vocalisations were recorded with a Marantz PMD661 Portable Stereo recorder with directional microphone and a compact Sony handheld recorder.

2.3.3 Other variables

Other than predation risk, many factors, including resource availability and habitat type, may constrain primate behaviour. The following variables were recorded as possible predictors of observed behavioural variation and, where appropriate, were incorporated in models as covariates.

Table 2.2. List of monkey variables recorded at each encounter

Monkey variables recorded	**Variable description**
Time before detection	Minutes until detected by monkeys (max 5 minutes)
Time till fleeing after detection	Minutes till monkeys are completely out of sight (max 20 minutes)
Group size	Number of individuals counted
Polyspecific	yes no
Number of species present	Between 0 and 6
Other species	Diana monkey Lesser spot-nosed monkey Campbell's monkey Sooty mangabey Red colobus Black and white colobus
Height off ground	Ground level 0 - 5 m 5 - 15 m 15- 25 m 25 - 50 m
Group cohesion	Isolated Paired Multiple
Reaction distance	Distance in metres at which monkeys detect the observer
Flight Initiation Distance (FID)	Distance in metres at which monkeys run away at the approach of the observer
Visibility before and after detection (score between 1- 8 visible body parts per individual)	Head Higher abdomen Lower abdomen Left arm Right arm Left leg Right leg Tail
Presence of freezing	yes no
Presence of vocalisation (both alarm calls and contact calls)	yes no
Presence of movement	yes no
Reaction category	No reaction Vocalisation, inspection, no movement Vocalisation, inspection, movement Inspection, fleeing Vocalisation, fleeing Immediate fleeing
Vocalisation before and after detection	Audio recording

2.3.3.1 Habitat

Habitat structure can be an important factor in influencing primate behaviour. In order to assess the potential impact of habitat, transects were walked a second time following the behavioural observations to collect a set of forest habitat covariates. Quadrats of 5 m x 5 m were placed every 500m to collect data on overall habitat characteristics of the surveyed area (n=298). Within each quadrat, number of trees (defined as plants with a woody trunk and lateral branches) with different diameters at breast height (DBH), mean tree height (mean of all trees within quadrat with DBH > 6 cm), undergrowth visibility, canopy density and slope were recorded (Table 2.3).

Tree height was measured using a rangefinder (ELEPHAS handheld digital laser tape measure – 40m) and DBH of trees was measured using a tape measure (Silverline MT45 - 30m). Undergrowth visibility was measured using a 1m x 1m checkerboard divided into 10 cm squares (Coleman and Hill 2014), and canopy density was measured using a dotted transparent layer. Habitat data was also recorded in the same way at each location were monkeys were observed, following the behavioural data collection.

2.3.3.2 Resource availability

To estimate food availability, presence/absence of fruit on the ground was recorded within each quadrat.

2.3.3.3 Other

Weather conditions (i.e. presence of clouds/sun) were recorded as potentially impacting visibility and detectability of monkeys. Time of day and time of year were also recorded.

Table. 2.3 List of habitat variables collected at each habitat plot

Habitat covariate	Variable description
Mean tree height	Mean height of all trees in plot with DBH > 6 cm
Canopy cover	Number of dots visible against the sky when transparent layer is held up from the centre of the plot. This was then converted into a %
Undergrowth visibility	Number of 10 cm squares visible when checkerboard is held in each corner of plot and observer is standing at a 5 m distance
Slope	Slope of plot, visually estimated as: Flat (0) = slope 0-10°, Slight (1) = slope 11-25°, Moderate (2) = slope 26-45°, Steep (3) = slope > 45°
Habitat type	Categorised as IPF = Intact Primary Forest, DPF = Degraded Primary Forest, MSF = Mature Secondary Forest, YSB = Young Secondary Bush, FRG = Forest on Rocky ground
Trees DBH 1-5 cm	Number of trees with a diameter of 1-5 cm present within plot
Trees DBH 6-10 cm	Number of trees with a diameter of 6-10 cm present within plot
Trees DBH 10-30 cm	Number of trees with a diameter of 10-30 cm present within plot
Trees DBH 30-50 cm	Number of trees with a diameter of 30-50 cm within a 50 m radius
Trees DBH > 50 cm	Number of trees with a diameter of >50 cm within a 50 m radius
Water features	Presence and type of water features within 20 m of habitat plot: river/stream, standing water (pond/lake), swamp

2.4 Data processing and analysis

As some of the habitat variables (Table 2.3) are likely to be correlated, a principal component analysis (PCA) was initially carried out hoping to reduce

the number of components and to check for collinearity amongst habitat descriptors. The data used for the PCA was derived from the habitat plots spaced every 500m along the transect lines (excluding monkey plots). In the first PCA, a strong correlation was found between the larger categories of trees (DBH=30-50 cm and > 50 cm) and between the smaller categories of trees (DBH=1-5 cm and 6-10 cm). Following this result, the two larger categories and the two smaller categories of trees were joined resulting in two predictors (number of small trees with DBH=1-10 cm and number of large trees with DBH > 30 cm), thus reducing the number of predictor variables. Slope was removed from the PCA as it was considered unlikely to have an effect on monkey behaviour, this variable was originally recorded as a potential predictor of monkey distribution. Another PCA was run with the five remaining habitat variables: mean tree height, canopy cover, undergrowth visibility, number of small trees and number of large trees (Appendix 1, Figure A1.1). The first 2 principal components of the PCA, however, only explained 58.7% of the variation and therefore habitat variables were included separately in models, where relevant (Table 4.1 and 5.1).

Vocalisations were processed by listening to audio recordings and marking all Diana monkey calls recorded before and after detection, these were then converted into number of calls per minute by dividing number of calls counted by the number of minutes of each recording. Calls were classified as either contact calls or alarm calls. All calls classified in Candiotti et al. (2012) as A, LA, HA were marked as contact calls. Calls classified in Candiotti et al.

(2012) as RA (alert call), plus female and male alarm calls were all marked as alarm calls (Figure 2.8).

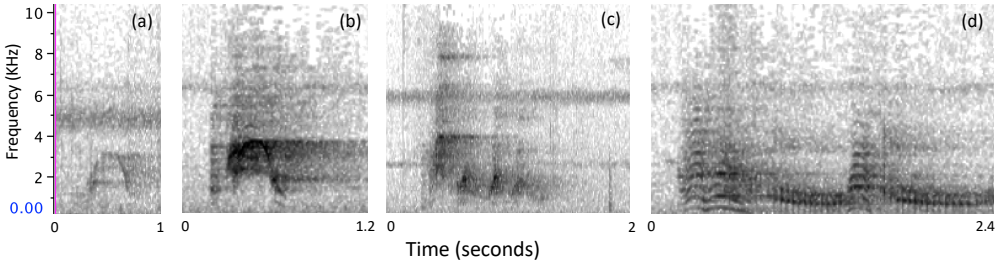

Figure 2.8 Example spectrograms showing different types of Diana monkey calls: female contact call (a), female alert call (b), female leopard alarm call (c), male leopard alarm call (d).

To assess which hunting pressure map, if any, best predicts behaviour in monkeys, a series of candidate models were built, each with a different hunting predictor (law enforcement area, distance to settlements, encounter rate of hunting signs and gunshot frequency) and all combinations of relevant covariates (Table 4.1 and 5.1). Collinearity of predictor variables was assessed, and all candidate models were checked for residual errors. For all behavioural variables, selected models, including a null model, were then compared with an information theoretic approach corrected for small sample size (AICc) (Burnham and Anderson 2002). Models with $\Delta AICc \leq 2$ were deemed equally supported and thus model averaging was carried out to obtain model-averaged parameter estimates. Where more than one hunting predictor was present in the top models, collinearity was checked before model averaging. As data on gunshot frequency was not available for all observations, the overall sample size was initially reduced to compare all hunting pressure predictors. When gunshot frequency was not present as a predictor in the top models, this variable was removed and subsequent

analysis was conducted on the full dataset using three predictors of hunting intensity which were available across the study area: law enforcement area, distance to settlements and encounter rate of hunting signs. All statistical analysis was carried out in R Studio version 1.1.456 (R Core Team 2018). Packages used include "MuMIn" for model averaging: function "model.avg" and package "stats" for PCA: function "prcomp". Maps were made using QGIS mapping software version 3.4.2-Madeira (QGIS Development Team 2018) and package "ggplot2" (Wickham 2016) in R Studio. Further details on data processing and analysis are described in the relevant chapters. Methods for building and running agent-based model are fully outlined in Chapter 6.

2.5 Challenges and reflections

Conducting fieldwork in rural areas of West Africa poses its own set of challenges. I was very fortunate to have great contacts in both countries, which made organising the logistical aspects a lot easier. Travel back and forth between countries and between field sites and towns required significant coordination with vehicles and local organisations. Furthermore, given the poor conditions of many roads, travel required extensive time. In Liberia, movements between the field site in Gola and the capital Monrovia were coordinated with the support of the executive director of SCNL Michael Garbo. In Sierra Leone, transport to Gola from Kenema was organised with the help of Benjamin Barca, research advisor for the GRNP at the time of study. Benjamin Barca also helped to coordinate the deployment of

Audiomoth recording devices in Sierra Leone as well as with my accommodation whilst in Kenema. In Monrovia, GolaMA project manager Anne Gardner and Wild Chimpanzee Foundation (WCF) Country Director Annika Hillers, both helped with my accommodation and other logistics whilst in the city. Benjamin, Anne, and Annika all supported me throughout my time in West Africa, providing emotional support when needed and lots of useful advice.

During fieldwork, the biggest challenge was the management of different research teams of 5 to 8 people. In Sierra Leone the research team was composed of one trained research assistant working for the GRNP and 5-6 field porters and guides, members of communities around the forest. The team in Sierra Leone changed a lot, making it harder to establish ongoing relationships with people. The cook Mohammed Nyalley accompanied me on all trips in the GRNP in Sierra Leone. Fluent in English and very friendly, Mohammed was of great support to me during the fieldwork and helped me coordinate the team providing useful guidance. In Liberia the research team was a lot more consistent. Patricia Gaye, Mohammed Nyumalin and Emmanuel Yalla, members of Kungbor community, were core team members throughout my fieldwork in Liberia (including during the pilot study). During my time in the field in Liberia, Patricia, Mohammed and Emmanuel became really good friends of mine, making fieldwork feel less repetitive and overall more enjoyable. As an ex-hunter, Emmanuel is extremely skilful in detecting and identifying monkeys, his help proved invaluable as he taught me many

aspects essential to my data collection, such as identifying species by their calls and moving around the forest in a stealthy manner.

Despite all the help and support received, inevitably some aspects of the fieldwork did not go according to plan. The study was initially going to include more detailed information on monkey behaviour (i.e. feeding, resting, grooming, vigilance) collected using a behavioural observations software. This was trialled during the pilot study but unfortunately, given extremely low visibility within a tropical forest habitat and the strong wariness of the monkeys, it was almost impossible to observe the monkeys long enough to collect this type of data accurately. Additionally, the study was going to include a map of hunting pressure constructed using participatory mapping techniques, by asking people to draw on a map the areas used for hunting (present and past). The GFNP in Liberia, however, was being demarcated during the time of fieldwork, leading to conflict in some areas between the park management and local communities. This was deemed a very sensitive time to ask people about their hunting practices and therefore data for this map was not collected as it would likely be inaccurate. Despite a few holdbacks however, fieldwork was conducted with only minor issues and the overall experience was an extremely positive one.

Chapter 3

Multiple methods of mapping hunting pressure in the Gola Forest of West Africa indicate different patterns of hunting distribution

3.1 Introduction

Tropical forest ecosystems are increasingly recognized as severely threatened by human hunting pressure (Milner-Gulland et al. 2003; Wilkie et al. 2011; Ripple et al. 2016; Brashares and Gaynor 2017). In many countries, unsustainable hunting is leading to extensive overexploitation of wildlife, with devastating effects on species numbers and cascading effects on community composition and ecosystem function (Wilkie et al. 2011; Kurten 2013; Ripple et al. 2016). The concept of the "Empty Forest" , first introduced by Redford in 1992, evokes an ever more fitting reality, with defaunation trends worsening across the earth's tropical belt (Peres 2009). Increasing evidence supports the idea that an intact forest does not necessarily indicate an intact ecosystem (Milner-Gulland et al. 2003; Harrison 2011; Wilkie et al. 2011). The primary cause of this trend is the rise in commercial hunting and trade, fuelled by population growth and demand and often led by non-local people (Kuehl et al. 2009). Since at least 40 years, in fact, hunting patterns have shifted away from small scale, locally conducted subsistence hunting

(Robinson and Redford 1994; Kuehl et al. 2009; Benítez-López et al. 2017). Together with advances in hunting technologies and better road infrastructure, which aids accessibility to tropical forest habitats, the commercialisation of hunting is exacerbating the anthropogenic impact on tropical wildlife (Wilkie et al. 2011). Some alarming figures recently estimated a reduction in abundance of up to 83% in mammals and 58% in birds in hunted areas compared to unhunted areas in the tropics, mainly driven by the increase in hunting for a monetary profit (Benítez-López et al. 2017). Ape populations in Gabon, for example, declined by more than 50% between 1983 and 2000, again primarily due to commercial hunting and Ebola virus (Walsh et al. 2003).

It follows that there is a clear urgency to monitor hunting pressure patterns in order to assess the sustainability of offtake and the efficacy of conservation interventions (Sutherland 2001). Measuring the temporal and spatial extent of hunting is an important step in understanding its impact and in evaluating the effectiveness of protection, following the implementation of project interventions (Fa et al. 2005). However, despite increasing awareness and evidence to support the extent of the issue, determining the distribution and intensity of hunting remains extremely challenging. Hunting can be considered as a non-structural form of habitat disturbance with few clear measurable signs (i.e. unlike deforestation) (Peres et al. 2006). Hunting, in fact, is recognised as an almost undetectable threat which is very difficult to quantify, due to large amount of effort involved in monitoring the relatively few visible signs of its incidence (Peres et al. 2006; Jones et al. 2017). So

what methods are currently used to assess hunting patterns, and what are the benefits and drawbacks of each of them? By reviewing all papers which measure hunting published within five main conservation journals (Biodiversity and Conservation, Biological Conservation, Biotropica, Conservation Biology and Oryx) over the past 10-years (2009-2019), it becomes apparent that a diverse array of methods is applied to estimate hunting distribution and intensity, and that the majority of studies select only one method (Figure 3.1).

Level of protection has often been used as an indirect indicator of hunting pressure (Effiom et al. 2013; Rosin and Swamy 2013), as on the ground enforcement is assumed to reduce hunting efforts in those areas. There is evidence, however, that protected areas do not always have effective law enforcement (Laurance et al. 2012; Tranquilli et al. 2014). Specifically, in Africa, protected areas suffer from high levels of infiltration by hunters, with conservation efforts and protected area management being very low or non-existent in some areas, primarily due to inadequate funding and low resource availability (Bruner et al. 2001; Baghai et al. 2018). The extent of this infiltration is not always known, highlighting the importance of finer scale monitoring of hunting patterns (Fa and Brown 2009). Furthermore, patrol deployment, which has been shown to significantly improve the effectiveness of protected areas (Hilborn et al. 2006), is often heterogeneous across a park (N'Goran et al. 2012).

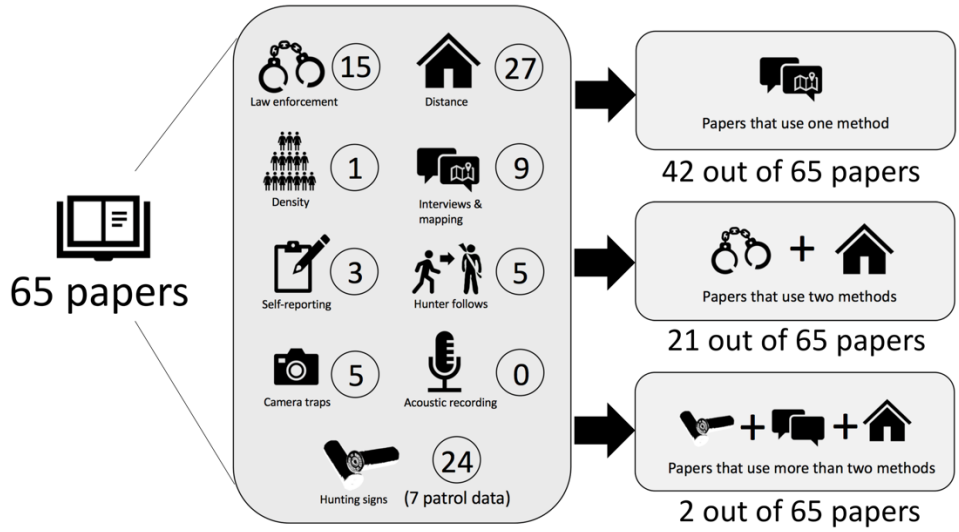

Figure 3.1 Methods used to estimate distribution of hunting intensity, showing the number of papers that use each method and the number of papers that use more than one method. Data derived from all papers published in five conservation journals over the past 10 years (2009-2019). **Law enforcement**: using level of protection as a proxy for hunting intensity; **Distance**: using distance to human infrastructure as a proxy for hunting intensity; **Density**: using number of inhabitants at each location to infer hunting intensity; **Interviews & mapping**: asking hunters where they hunt (i.e. how far, what direction, which areas, mark kill locations on a map); **Self-reporting:** asking hunters to self-report hunting locations (i.e. through self-monitoring forms); **Hunter follows:** following hunters on hunting trips; **Camera traps:** recording detections of hunters; **Acoustic recording:** recording frequency of gunshots; **Hunting signs:** recording signs of hunting (i.e. gun shells, snares) along transect lines or opportunistically along hunting trails

Another simple measure of hunting pressure is distance to human habitation or infrastructure (Hill et al. 1997). A broad body of literature has used central-place foraging theory to describe human hunting pressure patterns (Peres and Lake 2003; Yackulic et al. 2011; Abernethy et al. 2013; Constantino 2016). This theory is based around the idea that humans return to a central place (village or community) after hunting trips, and thus will exploit regions near to this central place to a greater extent. An inverse relationship between distance from human settlements and hunting intensity is therefore expected. Distance to access points, roads and other human infrastructure have also been used as indirect indicators of hunting intensity (Kuehl et al. 2009; Murai

et al. 2013; Whytock et al. 2014; Constantino 2016). This relationship, however, may not always hold true, as overexploitation is causing hunters in many places to venture further from their homes to find prey (Robinson et al. 2011), often undergoing trips of multiple days and using hunting camps within the forest as a base. Furthermore, with the rise in commercial hunting, non-local hunters may exploit wildlife at far away locations and thus hunter movement patterns are not necessarily correlated with the distribution of local villages (Kuehl et al. 2009). The advantage of indirect measures of hunting intensity is that they can be calculated with little effort and give a good first indication of potential hunting patterns when limited resources are available. These broad classifications and qualitative descriptions, however, do not account for finer scale spatial and temporal variation in hunting, which are essential to fully understand true interactions within this predator-prey system.

Although proxies for hunting pressure such as protection level and distance to human infrastructure are easy to calculate, monitoring direct signs of hunting occurrence allows identification of finer scale patterns. The main method used to assess heterogeneity of hunting pressure is to record hunting signs, such as empty gun shells and snares (Laurance et al. 2008; Cronin et al. 2016; Trolliet et al. 2017). If these are recorded systematically along transect lines, density or encounter rates per km can then be calculated, and spatio-temporal variation across a landscape can be assessed, if sufficient coverage is deployed and monitoring is repeated (Linder and Oates 2011; O'Kelly et al. 2018). Some studies have also used camera traps to record

encounter rates of hunters as an indicator of hunting intensity (Brodie et al. 2015; Macdonald et al. 2018). The amount of effort involved in this type of census however can be large, and financial and time constraints are likely to have a big impact on the methods chosen. Hunting sign data is therefore frequently collected opportunistically and in conjunction with other monitoring (i.e. ranger patrols) and thus is harder to use quantitively (Keane et al. 2011).

Hunting intensity has also been measured by working alongside hunters within communities. Through interviews, self-monitoring forms, hunter follows/tracking and participatory mapping, many studies have collected information on hunting practices, species hunted, total numbers harvested as well as main location of hunts (Sirén et al. 2004; Thoisy et al. 2005; Peres and Palacios 2007; Rist et al. 2009; Shaffer et al. 2017). Interview data is invaluable, as it aids understanding of the main socioeconomic drivers of hunting and gives an insight into the diversity of hunting traditions and motives (Borgerson et al. 2016; Whytock et al. 2018). In certain contexts, however, issues related to the illegality of hunting may lead to inaccurate reporting by hunters and thus caution should be taken when interpreting results (Nuno et al. 2013). Furthermore, it is difficult to gain spatially explicit data on the intensity of hunting, with studies often focussing on village catchment areas and inferring variation in spatial intensity using a distance metric (Zapata-Ríos et al. 2009).

A newer method is passive acoustic monitoring (PAM) to record frequency of gunshots across a landscape (Wilkie et al. 2016; Astaras et al. 2017; Prince et al. 2019). Until recently, widespread use of recording devices was primarily limited by the cost of purchasing equipment, which was exceedingly high. Cheaper alternatives however, are being developed at a growing rate (Whytock and Christie 2017; Beason et al. 2018; Hill et al. 2018), suggesting this method may gain increasing popularity in the next few years. The advantages are that it allows for the collection of high-quality fine scale spatial data on patterns of gun hunting, producing reliable outputs of hunting intensity at a specific time and place. The main limitation is the large amount of effort involved both in the deployment of devices, often to remote locations, and in the processing of the resulting audio files to extract gunshots. Algorithms to automatically detect gunshots from audio files have recently been developed (Wrege et al. 2017), but the high rate of false positives means processing to verify selected gunshots remains time consuming.

Effort required often becomes a limiting factor when trying to select which hunting pressure indicator to use, especially in practical management contexts. This has led to the majority of studies only using one method. However, a comparative evaluation of different methods is lacking. The aim of this study is to compare hunting pressure maps of the same region built using different methods, to highlight commonalities and differences, and to draw attention to the possible difficulties researchers and practitioners may encounter when attempting to quantify spatial variation in hunting across a region. Maps of hunting pressure across the Gola Forest landscape in Liberia

and Sierra Leone were derived using three indicators: 1) distance from human settlements, 2) encounter rate of hunting signs, and 3) frequency of gunshots. These three methods were chosen due to accessibility of data and were considered the most viable at the time of study. Given the differences between Gola forest areas highlighted in Chapter 2 (*2.1. Study Site, 2.1.1 Location*), hunting pressure is expected to be lower in the Gola Rainforest National Park (GRNP) of Sierra Leone and higher in both the Gola Forest National Park (GFNP) and the community forest of Liberia. The resulting maps of hunting pressure were then assessed with respect to the three levels of law enforcement within the region.

3.2 Methods

3.2.1 Distance from human settlements

To build a map of hunting pressure based on distance from human settlements, a *kernel density estimation (KDE)* approach was implemented (Wand and Jones 1994). KDE is a spatial analysis technique that measures the location of point features relative to each other and displays the distribution of a variable by smoothing it on a continuous surface (King et al. 2015). Using coordinates of settlements as point features, kernel density estimators can be used to construct maps of hunting pressure as a function of distance from communities.

To construct a map of hunting pressure for the Gola region using the KDE approach, firstly all locations of forest communities surrounding the Gola region were collated (Figure 3.2 a). For the GRNP in Sierra Leone, settlements were those defined as 'forest edge communities' by the 2010 REDD project assessment (Bulte et al. 2013). For Liberia, the settlements surrounding the study region were collated by the Society for Conservation of Nature in Liberia (SCNL). Where possible hand-held GPS coordinates of the communities were recorded and when missing, coordinates were collated from the most recent and accessible census available (Liberia Institute of Statistics and Geo-Information Services, national population census 2008).

Kernel bandwidth was calculated using information on distance travelled from settlements by hunters in Liberia. This data was collected across all of the GolaMa communities by Jones et al. (2018) as part of a hunter interview survey. Responses on maximum time walked to hunt were averaged across individuals to obtain mean maximum time walked in hours (2.9 h). This was then converted into km walked based on data on a 6km/h maximum walking speed by adult men (Oberg et al. 1993; Bohannon 1997), as hunters are primarily men and were observed to walk at a fast speed when travelling (personal observation). Thus 2.9 h was multiplied by 6 km/h to give 17.4 km. As the maximum time walked was averaged across individuals, it is likely that some individuals walked for longer periods than the reported mean. Therefore, the resulting number was doubled to ensure maximum hunting area was accounted for, obtaining a final kernel bandwidth (hunting search radius) of 35 km.

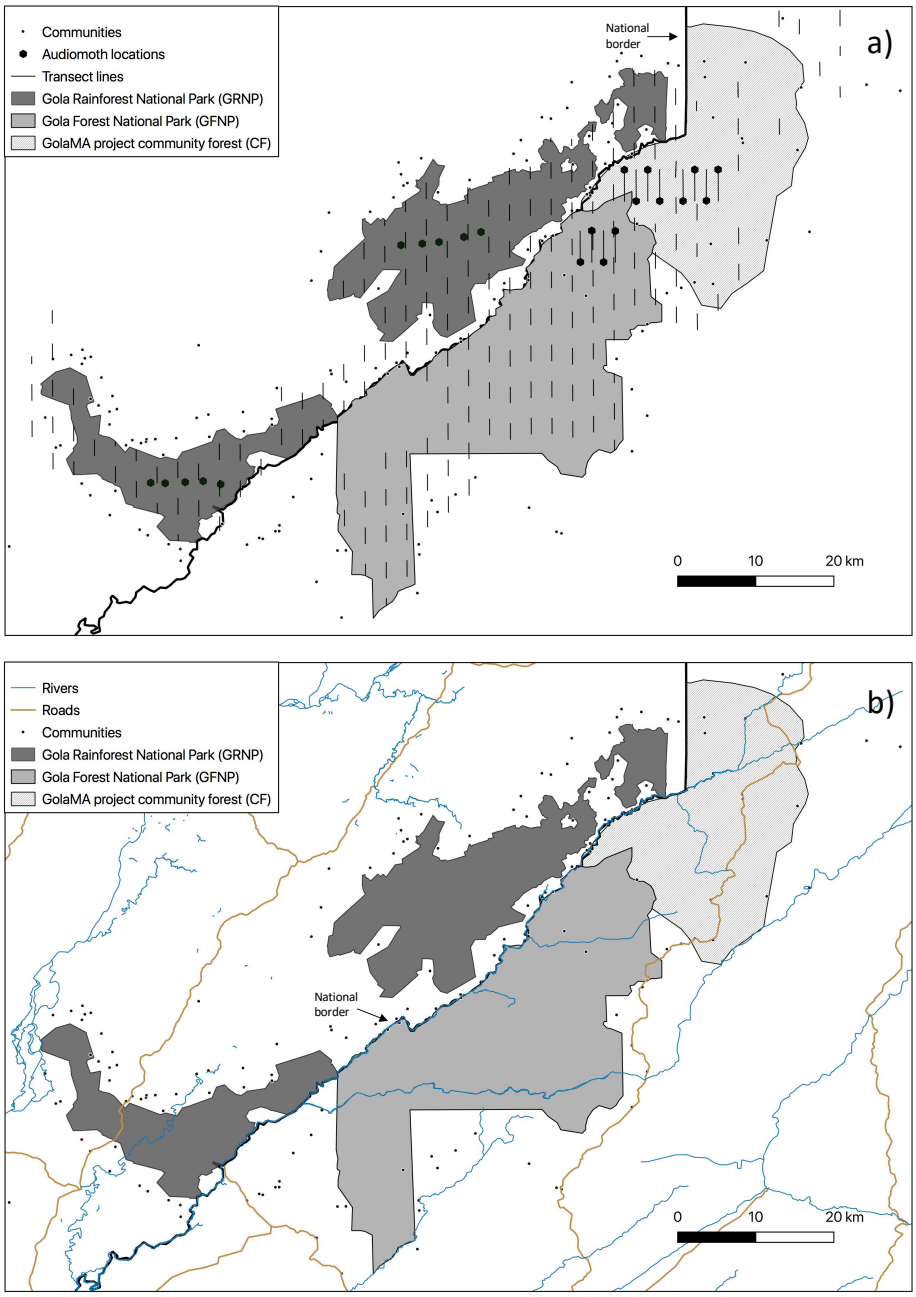

Figure 3.2 a) Distribution of transect lines used to collect hunting sign data, Audiomoth recording devices used to collect gunshot frequency data, and communities used to build the "Distance from human settlements" hunting map. **b)** Distribution of main roads and rivers in the study region

To account for variation in community size, data on number of households per settlement (collated from Bulte et al. 2012, the Liberian national population census 2008 and the Sierra Leone village survey conducted in 2016) was used to weight communities. A strong positive correlation of 0.74

between number of hunters and number of households in 15 communities surveyed as part of the GolaMa project (Spearman's rank correlation S= 146.92, n=15, p=0.002) (Appendix 2, Figure A2.1), supports the use of household number as an indirect indicator of hunting intensity for each community. For communities without information on number of households (n=36), median number of households across all other settlements was used.

3.2.2 Encounter rate of hunting signs

To build a map of hunting pressure using hunting sign data, *inverse distance weighted (IDW) interpolation* was used (Lam 1983). IDW interpolation assigns a higher weighting to nearby points and a lower weighting to points further away. The main underlying assumption is that points close to each other are more likely to be similar (O'Sullivan and Unwin 2010). This method was chosen as hunting pressure is expected to vary spatially across the region, but nearby points are expected to be similar. The IDW power coefficient, which specifies the distance weights, was chosen by assessing different values using leave-one-out cross-validation (O'Sullivan and Unwin 2010).

Data on hunting signs was collated from 3 datasets collected between 2011 and 2018 (Figure 3.2 a). The datasets included were: Across the River Transboundary project (ARTP 2011-2012) survey, the GRNP 2015-2016 chimpanzee nest and hunting sign survey (Barca et al. 2018b) and the GolaMa 2016-2018 chimpanzee nest and hunting sign survey. Dataset survey regions were non-overlapping. When the same transect was repeatedly visited, only

data from the first visit was taken. In all datasets, survey design used standard distance sampling methodology along transect lines (Buckland et al. 2001).

Hunting signs recorded included empty gun shells, snares, hunter's trails, hunter's camps and machete marks. Empty gun shells and snares were recorded consistently across all datasets and therefore were selected to construct the hunting pressure map. Although hunter's trails were also recorded across surveys, these were not included due to uncertainty in the purpose of trails recorded as hunting trails, as many people may access the forest for different purposes. It was not possible to construct a density surface of hunting signs, as all distance sampling detection functions used showed a poor fit to the data and no significant predictors of hunting sign distribution were identified. Therefore, for each transect, the encounter rate of empty gun shells and snares per km was calculated and the values were assigned to point features at the centre of each transect. These centre points were then used for the IDW interpolation.

3.2.3 Gunshot frequency

Audiomoth recording devices (Hill et al. 2018) were placed at 22 fixed locations along permanent transect lines between March and May 2018 (Figure 3.2 a). Due to device failure, the final number of recording locations was 19. Each device was programmed to continuously record 24 h/day, with a sampling rate of 16kHz, resulting in a maximum autonomous recording period of 8 days. The short recording period was due to limitations in battery

life and logistics related to accessibility of locations. Devices were placed between 2-3 m above the ground within a 50 m radius of the coordinates set for deployment. The maximum detection distance for gunshots recorded by Audiomoth devices in dense moist evergreen and semi-deciduous forest was about 1 km, resulting in a total sampling area of approximately 60 km^2.

A total of 3216 h (134 days) of recordings were made across all sites. Audio data was processed using an automatic gunshot detection algorithm (Wrege et al. 2017). Potential gunshots were all verified both visually and acoustically due to the high number of false positives identified by the algorithm. Spectrogram scanning was also carried out for validation (Figure 3.3). To build a map of hunting pressure using frequency of gunshots, *IDW* interpolation was used, with point features matching the locations of the recording devices.

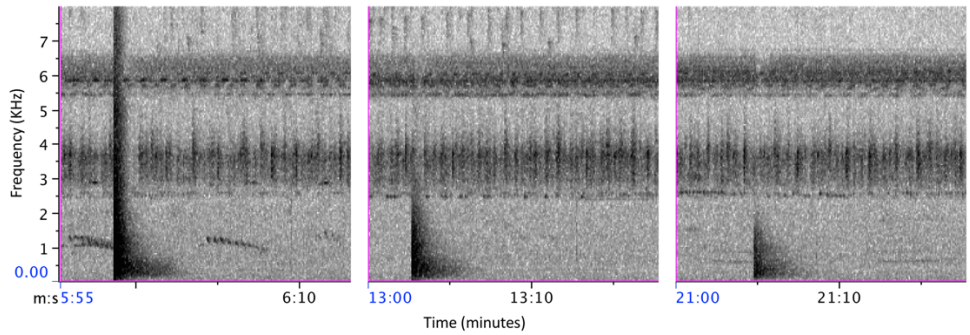

Figure 3.3 Example spectrograms showing gunshots at increasing distances from the Audiomoth recording device (from left to right: 100 m, 200 m, 400 m)

3.2.4 Map comparison

Each map was grouped according to level of law enforcement (community forest, GRNP and GFNP) and the different areas were ranked according to

intensity of hunting. Ranks were then compared to assess whether patterns of hunting pressure reflect expectations linked to park regulations and whether all maps result in the same ranking pattern.

All maps were then converted to a common index of 0 - 1 by subtracting the minimum value and dividing it by the maximum value for comparison. The resulting maps were compared both visually and by calculating a fuzzy numerical similarity statistic in the Map Comparison Kit software (Visser and de Nijs 2006). This method is equivalent to the Fuzzy Kappa method (Hagen 2003) for continuous rather than for categorical variables. Unlike cell-by-cell comparison techniques, fuzzy methods account for similarity between neighbouring cells, mimicking human judgment (Visser and de Nijs 2006). Alongside the statistic for overall similarity, this method yields a map specifying the degree of similarity, from 0 for total dissimilarity, to 1 for total similarity (Hagen 2003).

All analysis was carried out in R Studio v.1.1.456 (R Core Team 2018). Kernel density estimator analysis was performed in R using function sp.kde in the package "*spatialEco*" (Evans 2018). IDW interpolation was performed using function idw in the package "*gstat*" (Gräler et al. 2016). All maps were made using the package "*ggplot2*" (Wickham 2016). All audio processing was carried out in sound analysis software Raven Pro v.1.5 (Bioacoustics Research Program 2014).

3.3 Results

3.3.1 Distance from human settlements

A total of 158 settlements were collated across both countries (98 in Sierra Leone and 60 in Liberia) from the different sources. Size of settlement varied from 1 to 270 households, with a median of 14 and a mean of 30 households per settlement. Hunting pressure linked to distance from human settlements varied across the study region (Figure 3.4a), with an overall mean KDE of 0.65 ± SD 0.17 (range 0 - 1). In Liberia, the community forest area showed higher levels of hunting intensity compared to the GFNP (Table 3.1). In Sierra Leone, the northern and southern areas of the GRNP displayed higher levels of hunting intensity compared to central GRNP. Overall, hunting intensity appears high across the region.

3.3.2 Encounter rate of hunting signs

The 203 transect lines combined from all datasets resulted in a total of 410 km of survey effort (118 km in the GRNP, 53 km in the GRNP belt, 160 km in the GFNP and 80 km in the community forest) (Figure 3.2 a). A total of 181 hunting signs (99 empty cartridges and 82 snares) were extracted from the datasets. Mean encounter rate of hunting signs across the interpolated region is 0.46 ± SD 0.73 km^{-1} (range 0 – 3.5). Spatial patterns of hunting intensity appear fragmented and patchy (Figure 3.4b). A high proportion of the map displays low levels of hunting intensity due to the high numbers of

transects with no hunting signs detected. There are however clear clusters with a higher encounter rate of signs. In Liberia, these include various sampled patches within the community forest and in the northern GFNP. Despite the highest encounter rates being found in Liberia, the southern part of the GRNP in Sierra Leone shows two areas with a high number of hunting signs (Table 3.1). Patches with high encounter rates appear along the national border as well.

3.3.3 Gunshot frequency

A total of 159 gunshots were recorded across the 19 locations with a mean frequency of 1.17± SD 0.81 day^{-1} (range 0-8). The highest frequency of gunshots was consistently found in Liberia (Table 3.1). In central GRNP, however, a high frequency of gunshots was recorded in the western area and in southern GRNP a higher frequency of gunshots was recorded towards the border with Liberia (Figure 3.4c). A higher number of gunshots per day was recorded in the GFNP compared to the community forest (Table 3.1).

3.3.4 Ranking and comparison with degree of law enforcement

The distance map and the hunting sign map both identified the community forest as the area with highest hunting pressure and the GFNP in Liberia as the area with lowest hunting intensity (Table 3.1). Conversely, the gunshot map identified the GFNP as having the highest hunting intensity and the GRNP as having the lowest levels of hunting.

3.3.5 Map comparison

The results from the fuzzy numerical statistical comparison show low levels of agreement across all maps (Table 3.2). The distance map and the hunting sign map show only a 14% similarity, with similar areas (green in Figure 3.5a) corresponding mainly to areas of high hunting pressure. The hunting sign map and the gunshot frequency map show only an 18% similarity, with similar areas again corresponding mainly to areas of high hunting pressure (Figure 3.5b). The distance map and the gunshot frequency map show the highest level of similarity amongst all maps with a similarity statistic of 54%, mainly across high hunting pressure regions (Figure 3.5c).

Table 3.1 Mean and standard deviation of hunting intensity (derived from the different methods) according to area of law enforcement: Community Forest, GFNP: Gola Forest National Park, GRNP: Gola Rainforest National Park (north, centre and south). Mean KDE (± SD) for distance, mean encounter rate of hunting signs per km (± SD) and mean frequency of gunshots per day per device (± SD). Rankings of hunting intensity in parenthesis (1 is highest, 3 is lowest)

Location	Distance (KDE)	Hunting signs (km^{-1})	Gunshots (day^{-1})
Community forest, Liberia	0.75 ± SD 0.13 (1)	0.55 ± SD 0.88 (1)	1.16 ± SD 0.74 (2)
GFNP, Liberia	0.58 ± SD 0.10 (3)	0.33 ± SD 0.57 (3)	2.13 ± SD 0.61 (1)
GRNP, Sierra Leone	0.74 ± SD 0.11 (2)	0.54 ± SD 0.73 (2)	0.86 ± SD 0.71 (3)
North	0.96 ± SD 0.03	0.00 ± SD 0.00	--
Central	0.68 ± SD 0.08	0.63 ± SD 0.72	0.87 ± SD 0.89
South	0.77 ± SD 0.09	0.53 ± SD 0.79	0.85 ± SD 0.65

Table 3.2 Fuzzy numerical statistics (0 for total dissimilarity, to 1 for total similarity) comparing similarity between maps (neighbourhood = 4, exponential decay halving distance = 2). The number in parenthesis is the similarity statistics when comparing the uncropped region of the Kernel distance map and the hunting signs map

Map	Kernel Distance	Hunting signs	Gunshot frequency
Kernel distance	1.00	0.14 (0.20)	0.54
Hunting signs	-	1.00	0.18
Gunshot frequency	-	-	1.00

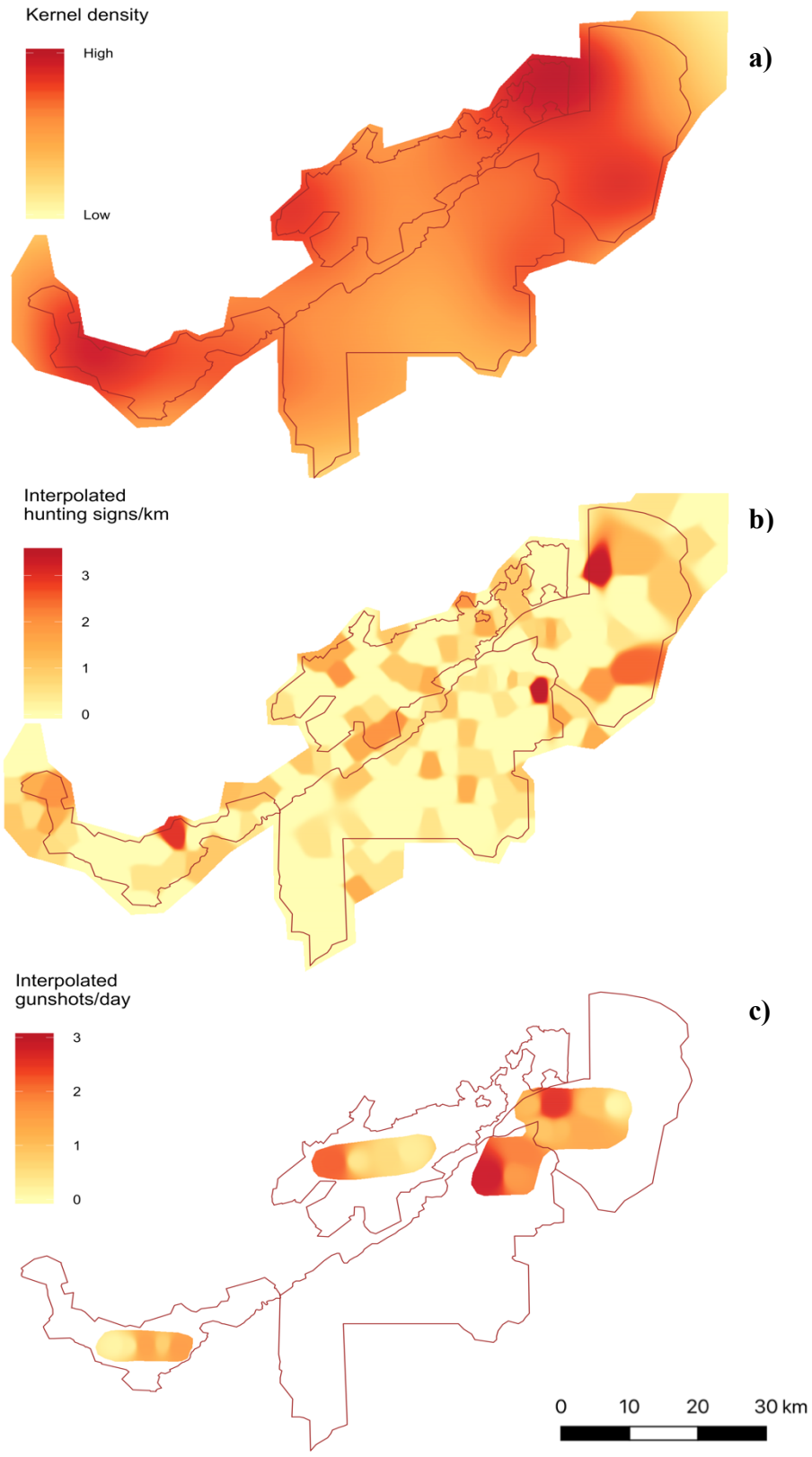

Figure 3.4 Maps of hunting pressure derived using **(a)** kernel density estimators of distance from communities (hunting pressure gradient from 0 (low) to 1(high)), **(b)** inverse-distance-weighted (IDW) interpolation from encounter rates of hunting signs per km and **(c)** IDW interpolation from frequency of gunshots per day.

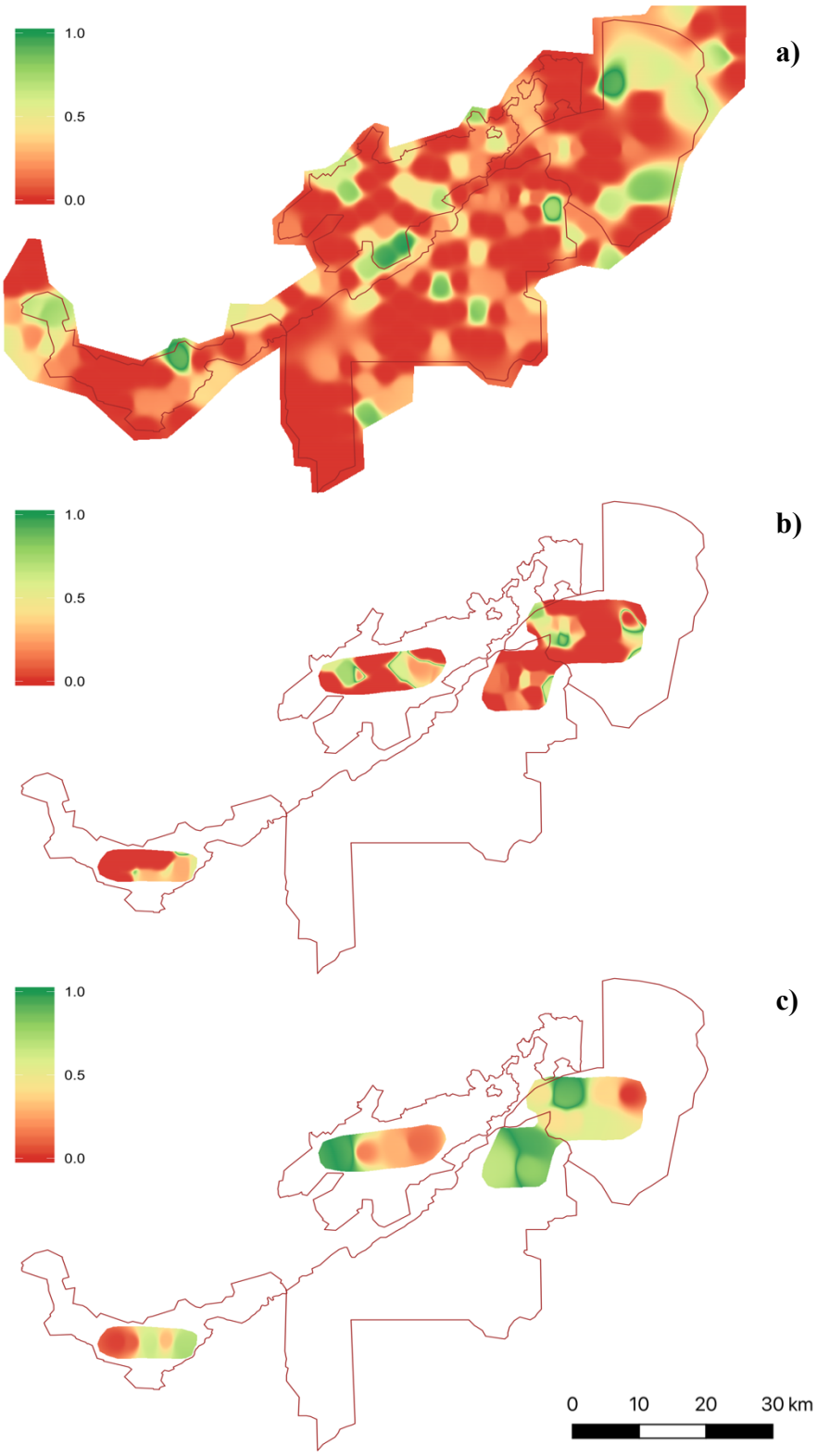

Figure 3.5 The fuzzy numerical similarity maps comparing **(a)** the distance map to the hunting sign map, **(b)** the hunting sign map to the gunshot map, and **(c)** the distance map to the gunshot map. Values of 1.0 (green) indicate total similarity and values of 0.0 (red) indicate total dissimilarity. Values of 0.5 (yellow) indicate some degree of similarity. The scale is a continuous gradient.

3.4 Discussion

There is evidence to suggest that heterogeneity in hunting pressure distribution affects sustainability, as determined by spatial interactions between hunters and prey species (van Vliet et al. 2010). Measuring hunting intensity on a fine spatial scale is therefore essential to capture patterns of species distribution, abundance and behavioural change (van Vliet et al. 2010). Quantifying spatially explicit hunting intensity can also help target specific areas under threat with stronger patrol effort and can aid the implementation of appropriate conservation measures (N'Goran et al. 2012; Risdianto et al. 2016). This study provides a broad comparison of different methods used to estimate hunting pressure across a landscape. Overall, the maps show very different patterns of hunting pressure distribution and each identify different law enforcement areas as having the highest level of hunting intensity. These findings highlight that the method chosen might fundamentally impact a studies' conclusions, and that a combination of methods might be favoured over the choice of just one. Furthermore, if only one method is chosen due to practical constraints, this should be reasoned by the intended objectives of the study, as different methods may be suitable in different contexts. Below, the benefits and drawbacks of each method are highlighted and suggestions on the appropriate use are made.

Given the limited resources usually available to conservation NGOs and management practitioners, distance to human infrastructure can provide a useful first assessment of expected broad hunting patterns. For example,

distance to human infrastructure can be a suitable covariate predicting large scale range-wide distributions for which fine scale data is difficult to obtain (Hickey et al. 2013; Ziegler et al. 2016). If used as a proxy for hunting intensity on a local scale, distance from human infrastructure should preferably be established as a good predictor of hunting pressure for that location. In Gabon, for example, Beirne et al. (2019) found that encounter rate of hunting signs decreased with distance to village and that villages had fairly small catchment areas (8 km) that rarely overlapped despite close proximity. In contrast, given the mean maximum distance travelled by hunters in the Gola forest (~17 km), the distance map in this study resulted in medium to high hunting intensity across the majority of the study region (Figure 3.4a, Table 3.1). The scattered presence of hunting signs throughout the area (Figure 3.4b) further suggests hunter accessibility is not primarily limited by distance to human infrastructure, and that other factors may be influencing hunter movement in Gola.

There are many other factors (i.e. level of law enforcement, habitat type, shifts in prey abundance) which may influence movement patterns and accessibility of hunters in different areas (Watson et al. 2013; Pereira et al. 2019). In Sierra Leone, the park is surrounded by many communities and, given its elongated shape, the distance map results in high levels of hunting intensity throughout (Figure 3.4a). This pattern, however, does not take into account on the ground patrolling which likely limits accessibility to the GRNP. The distance map identifies the community forest as the area with highest hunting intensity (Table 3.1). Since the community forest is not a protected area and therefore

communities are established within it and are legally allowed to hunt certain species, hunting pressure levels are indeed likely to be higher in this region. The GFNP, which is wider compared to the GRNP and is surrounded by fewer communities, shows the lowest levels of hunting intensity. Evidence from other maps, however, suggests high hunting intensity in this region (Table 3.1).

The relationship between human infrastructure and hunting patterns may also change within the same location as nearby resources are depleted, with evidence of trapping distance from communities increasing in just under a decade (Coad et al. 2013) and hunters reporting having to travel further away from a town in Central African Republic to find prey (Robinson et al. 2011). As a static measure, the distance map is unlikely to be a suitable long-term proxy of hunting pressure distribution in a changing world, as it cannot capture subtle changes in hunter movement. If attempting to evaluate the effectiveness of project interventions over time, distance to human infrastructure is unlikely to be a useful measure.

An effective method to monitor both fine scale spatial and temporal changes in hunting pressure is to record hunting signs. The hunting sign map provides useful fine scale patterns of hunting but likely underestimates hunting intensity. The map constructed using encounter rates of hunting signs (Figure 3.4b) is very patchy and fragmented, with low overall encounter rates of hunting signs per km due to the high number of transects with no signs detected. This is most likely because hunting signs are hard to detect and the

probability of seeing hunting signs on newly walked systematically placed transect lines is low. Human walking patterns, in fact, are not random (Boyer et al. 2012) and therefore the distribution of signs is likely linked to hunting paths. Consequently, low encounters can make this method impractical as a monitoring approach, because excessive levels of survey effort are required to identify changes through time (Jones et al. 2017). For temporal monitoring, transects can be repeated, however, as some studies have found evidence of transect use by hunters, an increasing number of signs when transect lines are repeated should be interpreted cautiously (Tagg and Willie 2013).

The hunting sign map does however highlight how different areas might compare relative to each other. The map identifies the community forest as having the highest hunting intensity, although encounter rates are surprisingly very similar to those in the GRNP (Table 3.1). The majority of hunting signs collected in the GRNP were empty shells (Appendix 2, Figure A2.2), which may have led to an overestimation of hunting occurrence, as it can be hard to age gun shells and therefore the dataset may be a reflection on both past and current hunting patterns. The GFNP is described as having the lowest hunting intensity (Table 3.1). The dataset that covered the area in the GFNP, however, was collected earlier (2011-2012) compared to the other datasets (2016-2018) and thus the results may not reflect more recent hunting pressure patterns, as evidenced by the gunshot map that identified high hunting intensity in this area. Combining both snares and gun shell encounters on the same map may also mask differences in the distribution between these two types of hunting practices. Tweh et al. (2014), for example, found that across Liberia gun-

hunting is more prevalent in forested areas and snare hunting is more common in areas without forest. The aim of this study, however, was to compare spatial patterns in hunting pressure as measured in the literature, with most studies combining multiple signs to infer hunting intensity (Linder and Oates 2011; Trolliet et al. 2017). Furthermore, when mapped separately, the gun shell encounter map still showed very low similarity with the gunshot map (Appendix 2, Figure A.2.2) suggesting the dissimilarities may be linked to differences in time of data collection.

Ideally, hunting sign data should be collected at a similar time for spatial comparison across a region. This is often very difficult in practice, as for many projects and park monitoring schemes, sustained large-scale hunting sign data collected systematically is limited, given the huge amount of effort involved. More frequently available data on hunting signs, collected by ranger patrols through CyberTracker (Cybertracker 2018) and SMART (SMART 2018) monitoring applications, still provides essential information crucial for park management (Farfán et al. 2019). These data are difficult to quantify given the opportunistic nature of the sampling, however modelling hunting sign occupancy from ranger patrol data can inform decision making (Vanthomme et al. 2016; Farfán et al. 2019), if paired with other systematic monitoring methods. Finally, if predictors of hunting sign distribution are identified, density surface maps of hunting signs can be estimated (O'Kelly et al. 2018).

Mapping the frequency of recorded gunshots provides the most precise data on gun hunting at the time of recording, with detailed information on hunting intensity per location as well as information on time of day of hunts (Appendix 2, Figures A2.3 & A2.4), which may aid targeted enforcement action (Astaras et al. 2017). The gunshot map (Figure 3.4c) shows a very high overall pressure from gun hunting in the study region. Converse to the results from the other maps, the gunshot map identifies the GFNP as having the highest hunting intensity, followed by the community forest area (Table 3.1). The spatial coverage of the gunshot map, however, is a lot smaller compared to the other two maps, and thus cannot capture the entire spatial extent of hunting across each area category. Nonetheless the GFNP was newly demarcated at the time of study (2018) and hunting pressure levels are therefore still likely to be high. The gunshot map identifies are some clear hunting hotspots in Sierra Leone, which in central GRNP coincide with areas closest to communities and in the southern GRNP with areas near the border with Liberia, where there is evidence of Liberian hunters crossing over into Sierra Leone (GRNP research assistants, personal communication). As an established protected area in Sierra Leone, the GRNP is expected to have lower hunting pressure compared to both areas in Liberia.

Due to the short deployment period, it is not possible to infer long-term temporal variation in hunting intensity from the data in this study. Passive acoustic monitoring, however, has the potential to capture long term changes in gun hunting intensity. Recording devices placed within Korup National Park in Cameroon over a 2 year period, for example, showed a 12% increase

in gun hunting which was not detected from the hunting sign line transect data collected in the same location (Astaras et al. 2017).

The main limitation of the gunshot map is the huge effort involved in device placement and audio processing as well as battery life of devices, which may limit the spatial and temporal extent of the monitoring. Technology however is advancing at an extremely fast pace and algorithms are being developed to pick up gunshots at the time of recording (Prince et al. 2019). This has the potential to substantially reduce processing time, data storage and battery life issues. Gunshot recordings, however, can only pick up patterns of gun hunting and therefore miss information on other types of hunting practices (such as trapping with snares), which have been shown to be carried out by different hunter groups (Jones et al. 2018). If the focus of the study is the distribution and abundance of species targeted with guns this may be appropriate, but acoustic monitoring is unlikely to provide useful insights for species mainly targeted with snares.

None of the above listed methods have a universal application and the suitability of a particular method will depend primarily on the aim and conservation goal of the study and on the resources available. It is not always feasible to choose the most suitable option, as cost and effort play a huge part in the decision process for NGOs, conservation programmes, researchers and park management (Walls 2018). Table 3.3 highlights which of the methods used in this study may be best suited to specific study aims and compares the cost, effort and amount of spatial and temporal variation captured by each method. The findings of this study highlight how different maps of hunting

intensity may yield very different results. Given the importance of accurately mapping hunting pressure for estimations of hunting sustainability and management, a combination of different methods may be advisable, within the context of a peer-reviewed literature that generally only selects one method. In the next two chapters the different maps are used to predict changes in behaviour induced by fear of humans, to assess which indicator might better predict behavioural change in two West African monkey species.

Table 3.3 Evaluation and main uses of the different methods used to estimate hunting pressure across a landscape. Cost: financial cost; Effort: data collection and analysis. Crosses give a relative qualitative measure for each category. Arrows indicate trends over time

Method	Cost	Effort	Spatial comparison	Temporal comparison	Aim and conservation goal of study
Distance	+	+	++	-	Large-scale comparison, first assessment of hunting patterns [if established as a significant predictor of hunting distribution: measure impact on hunted animals (abundance, distribution and behaviour)]
Signs	+++	+++	+++	++	Quantify spatial and temporal hunting patterns, evaluate effectiveness of interventions, inform targeted interventions, measure impact on hunted animals (abundance, distribution and behaviour)
Gunshots	+++ (↓)	+++ (↓)	+++	+++	Quantify spatial and temporal gun hunting patterns, evaluate effectiveness of interventions on gun hunting, inform targeted interventions, law enforcement tool (to catch hunters), measure impact on gun-hunted animals (abundance, distribution and behaviour)

Chapter 4

Does hunting affect the baseline behaviour of Diana monkeys, *Cercopithecus diana*, and lesser spot-nosed monkeys, *Cercopithecus petaurista*?

4.1 Introduction

All species adapt their behaviour to survive under different natural environmental pressures (Davenport 1984). This is true across the animal kingdom: the Arabian oryx, *Oryx leucoryx*, for example, forages mainly at night to avoid the desert heat (Williams et al. 2001), and many bird species migrate thousands of miles each year to find food (Alerstam 1993). Given the accelerating environmental changes associated with the Anthropocene, animals are increasingly exposed to pressures linked to rising human populations and increasing development (Tuomainen and Candolin 2011).

Just as natural environmental pressures drive behavioural change, so do human induced pressures such as loss or fragmentation of habitats, human disturbance and hunting pressure (Wong and Candolin 2015; Otto 2018). These pressures carry potential strong impacts on the overall fitness of animals, as behavioural change can have high energetic costs (Amo et al. 2006). The Iberian frog, *Rana iberica*, for example, increases its vigilance

levels near human recreational areas, consequently reducing resource use (Rodríguez-Prieto and Fernández-Juricic 2005). Two turtle species (*Terrapene carolina and T. ornata*) avoid road infrastructure within an increasingly fragmentated landscape in Illinois (USA), potentially leading to a significant negative effect on gene flow (Shepard et al. 2008). In recent years, an increase in commercial hunting and trade is leading to extensive overexploitation of many species (Fa et al. 2002; Milner-Gulland et al. 2003), with consequent effects on prey density and behaviour (Verdade 1996; Peres and Palacios 2007; Ciuti et al. 2012).

Predation often leads to the development of antipredator behavioural adaptations in prey species (Caro 2005). These can be broadly grouped into primary/ baseline defences (the focus of this chapter), which animals display to minimise detection regardless of predator presence, and secondary/reaction defences (the focus of the next chapter), which animals display during an encounter with a predator to defend themselves from attack (Edmunds 1974). There are many baseline adaptations that prey can adopt to minimise the chance of being detected by predators. These can include, amongst others, increasing vigilant behaviour to help detect predators in advance, altering timings of activity patterns to when predators are less active, selecting 'refuges' or strata that do not overlap with those of predators or that represent areas of shelter and reducing vocalisation levels to minimise conspicuousness (Caro 2005). These cryptic adaptations are more likely to occur against pursuit predators such as humans that hunt using acoustic cues (in contrast with prey responses to ambush predators which rely on signalling detection

via conspicuous behaviour) (Lima 1998; Kavaliers and Choleris 2001). Thus, in the context of human predation, we would expect an increase in baseline defences in prey that reduce the chances of being detected in areas with high hunting pressure.

Higher vigilance increases the chances of detecting a predator (Dehn 1990), therefore you would expect higher vigilance levels in areas under greater predation risk. Blue tits, *Parus caeruleus*, for example, increase their scanning rates where predation risk is higher (Lendrem 1983). Similar patterns have been found as a result of human predation in both ungulates and birds. In Zimbabwe impalas, *Aepyceros melampus*, spend more time being vigilant in properties with a higher level of hunting pressure (Matson et al. 2005). Casas *et al.* (2009) found an increase in time spent vigilant by lapwings, *Vanellus vanellus*, golden plovers, *Pluvialis apricari,* and little bustards, *Tetrax tetrax,* on days when humans hunted in agricultural areas of southwestern France.

Finding areas of refuge and reducing overlap with predator locations can also help reduce prey detectability (Caro 2005), therefore reduced overlap between predator and prey strata use may be expected under greater predation risk. An endangered Hawaiian forest bird, *Chasiempis ibidis*, for example, significantly increases its nesting height in response to an increase in rat predation (Vanderwerf 2012). Samango monkeys, *Cercopithecus mitis erythrarchus*, seek refuge high in the canopy to decrease risk of being predated upon by terrestrial predators (Coleman and Hill 2014). Similarly,

species may seek refuge in thick vegetation to minimise detection probabilities by reducing their overall visibility (Caro 2005). Male red deer, *Cervus elaphus*, for example, moved to dense concealing tree cover at the onset of the hunting season in central Norway (Lone et al. 2015). Another way to reduce detectability is to reduce overall vocalisation levels (Caro 2005). A study in great tits, *Parus major*, found that birds decrease their singing for a few days following exposure to a predator (Abbey-Lee et al. 2016). Therefore, if predation is consistently high, this "carry-over effect" may lead to a constant reduction in call rate, providing that the benefits of reduced detectability outweigh the cost of reduced vocalisation. Diana monkeys, *Cercopithecus diana*, however, do not differ in their overall calling frequency before a playback experiment between a hunted and an unhunted site in Taï National Park (Bshary 2001). It is therefore likely that this pattern will vary depending on the species and the location.

Variation in group size is also often associated with predation pressures. According to the 'many-eyes' hypothesis (Pulliam 1973; Lima 1990), increased vigilance in larger groups increases the chances of detecting a predator, furthermore the 'dilution effect' hypothesis proposes that the likelihood of being targeted as an individual is reduced when more individuals are present (Lima 1990). Both these theories suggest pressures would act to increase group size as an antipredator strategy. Fish schools and bird flocks, for example, rely on large numbers to reduce the individual probability of attack (Caro 2005). On the other hand, larger groups are more conspicuous and are thus more likely to be detected by predators, suggesting

a selection for smaller groups to minimise attack rate (Cresswell and Quinn 2010). In the context of baseline defences that reduce the probability of detection we might expect pressures for smaller group sizes as a result of human predation. The snub nosed langur, *Simias concolor*, for example, lives in smaller groups in areas with high levels of hunting and in larger polygamous groups in areas with reduced hunting pressures (Watanabe 1981). Eider ducks, *Somateria mollissima*, formed an optimal group size in relation to hunting density, decreasing or increasing numbers depending on season and food necessity and balancing the trade-offs of group size under specific hunting conditions (Laursen et al. 2016). Similarly, the formation of mixed species groups has the same antipredator advantages of single species groups (Stensland et al. 2003). Diana monkeys and red colobus, *Piliocolobus badius*, for example, have been shown to associate as an antipredator strategy (Bshary and Noë 1997b). Again, to minimise conspicuousness against human pursuit hunters, polyspecific associations are expected to reduce with an increase in human predatory pressure.

As seen above, there is some evidence across the literature of changes in baseline defences with predation pressure. Predator-prey systems involving humans as predators, however, are unfrequently included in studies of antipredator behaviour (Berger-Tal et al. 2016). Yet you might expect human predation to have a huge effect on behaviour, given highly effective human hunting techniques which represent an ever-increasing threat. In areas where hunting by humans is more severe, resulting cryptic behaviours should thus be more pronounced. This chapter focusses on spatial variation in primary

baseline defences of Diana monkeys, *C. diana*, and lesser spot-nosed monkeys, *Cercopithecus petaurista*, as a result of varying levels of hunting pressure measured using different methods detailed in Chapter 3.

In many countries of west Africa, such as Liberia and Sierra Leone, increasing demands for wild meat have led to the exploitation of different primate species to unsustainable levels (Junker et al. 2012). Particularly in Liberia, hunting is a strong driver of primate species declines (Tweh et al. 2014; Ordaz-Németh et al. 2017). Few studies focus on behavioural change in primates linked to hunting by humans and these studies tend to compare the behaviour of a small number of groups or use a single method to estimate hunting pressure (Bshary 2001; Croes et al. 2006; Koné and Refisch 2007).

Here, baseline defences were recorded for multiple independent monkey groups across the region and different estimates of hunting pressure were used as predictors of behavioural patterns. The recorded behaviours were monkey height, visibility and vocalisation before detection, group size and number of species present. Monkey baseline defences are expected to vary as follows:

1. Monkey height is expected to increase in areas with higher hunting pressure, given that humans are terrestrial predators
2. Baseline visibility and vocalisation levels are expected to be lower in areas with higher hunting pressure

3. Group size and number of species present in a group are expected to decrease with an increase in hunting pressure

4. Behavioural differences related to hunting are expected to be more pronounced in Diana monkeys compared to lesser spot-nosed monkeys, as Diana monkeys are more vulnerable to human predation

4.2 Methods

For details on study site, study species, behavioural data collection and analysis see Chapter 2. The distribution of the surveyed transects is shown in Figure 4.1.

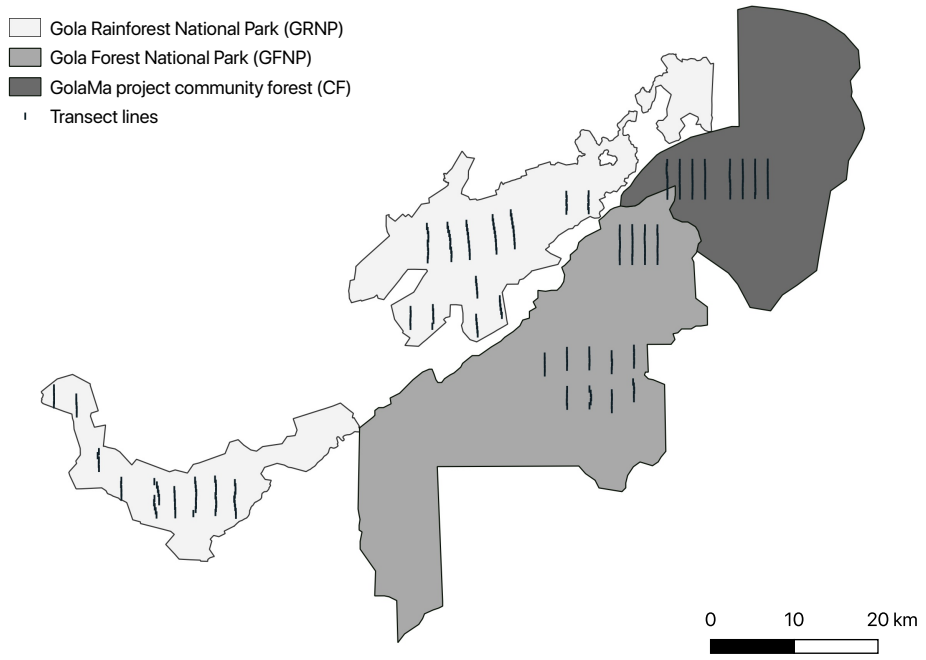

Figure 4.1 Location of surveyed transect lines across the study region

4.2.1 Statistical Analysis

The covariates added to each model, alongside reasons for inclusion, are listed in Table 4.1.

Analysis on monkey height in trees was conducted only with observations for which data on height before detection was available (Diana monkeys: n=51; lesser spot-nosed monkeys: n=22). Mean monkey height was calculated by taking the central value for each height category and then calculating the group mean. Monkey height was modelled using linear models with a Gaussian error structure.

Analysis on visibility was conducted only with observations for which data on visibility before detection was available (Diana monkeys: n=51; lesser spot-nosed monkeys: n=22). Visibility is defined as the total number of visible body parts (Table 2.2) divided by group size. A square root transformation (as the variable contains zeros) was carried out on visibility before detection to reduce spread and improve the normality of residuals. Visibility before detection was modelled using linear models with a Gaussian error structure.

Data on vocalisations was only collected for Diana monkeys, as this is a very vocal species. Analysis on baseline calls per minute was conducted only with observations for which recordings before detection were available (Diana monkeys: n=50). Baseline calls per minute were modelled using linear models with a Gaussian error structure.

As count data, group size was modelled using a GLM with Poisson error structure. In Diana monkeys, the resulting models were overdispersed and thus a GLM with a negative binomial error structure was carried out.

Analysis on number of species was conducted on a larger sample that included all observations where Diana monkeys or lesser spot-nosed monkeys were present (Diana monkeys: n=76; lesser spot-nosed monkeys: n=42). Number of species was considered an ordered variable and thus an ordinal logistic regression was fitted.

Gunshot frequency was only present as a predictor in top models for group size in Diana monkeys and for monkey height in lesser-spot nosed monkeys. For group size, both law enforcement area and gunshot frequency were present in top models; these predictors are collinear, hence for this case model averaging was not carried out and this analysis was not included in the thesis. For monkey height plotted residuals showed poor model fit, therefore only results from the complete dataset (i.e. not reduced for comparison with the gunshot frequency map) were included using the three predictors of hunting intensity which were available across the study area: law enforcement area, distance to settlements and encounter rate of hunting signs.

Parameter estimates and confidence intervals were derived from full model averaging of top models with $\Delta AICc \leq 2$. If a single best model was selected, then parameter estimates and confidence intervals from this model were reported. Reported mean estimates of different behavioural responses in the community forest (intercept) were derived from the averaged model, with all other variables held at an average.

Table 4.1 List of confounding variables selected to predict specific baseline defences in Diana monkeys and lesser spot-nosed monkeys in Gola

Response	Variable type	Variable	Reason for inclusion in model
Monkey height	Habitat variables	Mean tree height	Tree height likely influences monkey's height in trees
		Undergrowth visibility	Undergrowth density may influence monkey's height in trees
	Monkey variables	Number of species	Presence of other species may alter strata use
Visibility before detection	Habitat variables	Mean tree height	Higher trees likely reduce monkey detectability
		Undergrowth visibility	Reduced visibility likely reduces monkey detectability
	Monkey variables	Number of species	Lower perceived risk in poly-specific groups may reduce probability of hiding
Vocalisation before detection	Monkey variables	Number of species	Number of species likely influences vocalization levels
		Group size	Larger groups are likely more vocal
Group size	Habitat variables	Mean tree height	Higher trees likely reduce observer's detection of individuals, as monkeys are further away
		Undergrowth visibility	Reduced visibility likely reduces observer's detection of individuals
Number of species	Habitat variables	Mean tree height	Higher trees likely influences number of species present, also likely reduce observer's detection of different species
		Undergrowth visibility	Reduced visibility likely reduces observer's detection of different species
	Resource variables	Fruit presence	Presence of fruit likely increases probability of multiple species being present

4.3 Results

A total of 42 transects were surveyed during the study period, resulting in 134 km of survey effort: 62 km in the Gola Rainforest National Park (GRNP) of Sierra Leone, 34 km in the Gola Forest National Park (GFNP) of Liberia and 32 km in the community forest. A total of 58 *C. diana* observations were made on 37 transects, with 14 observations in the community forest, 15 observations in the GFNP and 29 observations in the GRNP. A total of 23 *C. petaurista* observations were made on 18 transects, with 6 observations in the community forest, 10 observations in the GFNP and 7 observations in the GRNP.

4.3.2 Monkey height

4.3.2.1 Diana monkey

Mean Diana monkey height in trees across the study region was 28.35 metres ± SD 6.85. Variation in height in Diana monkeys was best explained by four predictors (Table 4.2): two hunting variables (law enforcement area and distance to settlements) and two habitat variables (tree height and undergrowth visibility). Mean tree height was a strong predictor of monkey height (AIC weight = 1), with the height of Diana monkeys increasing by 0.61 metres (95% CI: 0.14 to 1.08) for every metre increase in mean tree height (Figure 4.2). Law enforcement area (Figure 4.3a) was not a good predictor of monkey height (AIC weight = 0.43). Height was intermediate in the

community forest (mean = 28.91; 95% CI: 26.01 to 31.80), increased by 0.46 metres in the GFNP (95% CI: -3.02 to 3.94) and decreased by 1.36 metres in the GRNP (95% CI: -5.55 to 2.82). Neither distance to settlements (parameter estimate: -0.78; 95% CI: -8.46 to 6.90, AIC weight = 0.12) nor undergrowth visibility (parameter estimate: 0.02; 95% CI: -0.10 to 0.15, AIC weight = 0.28) were good predictors of monkey height.

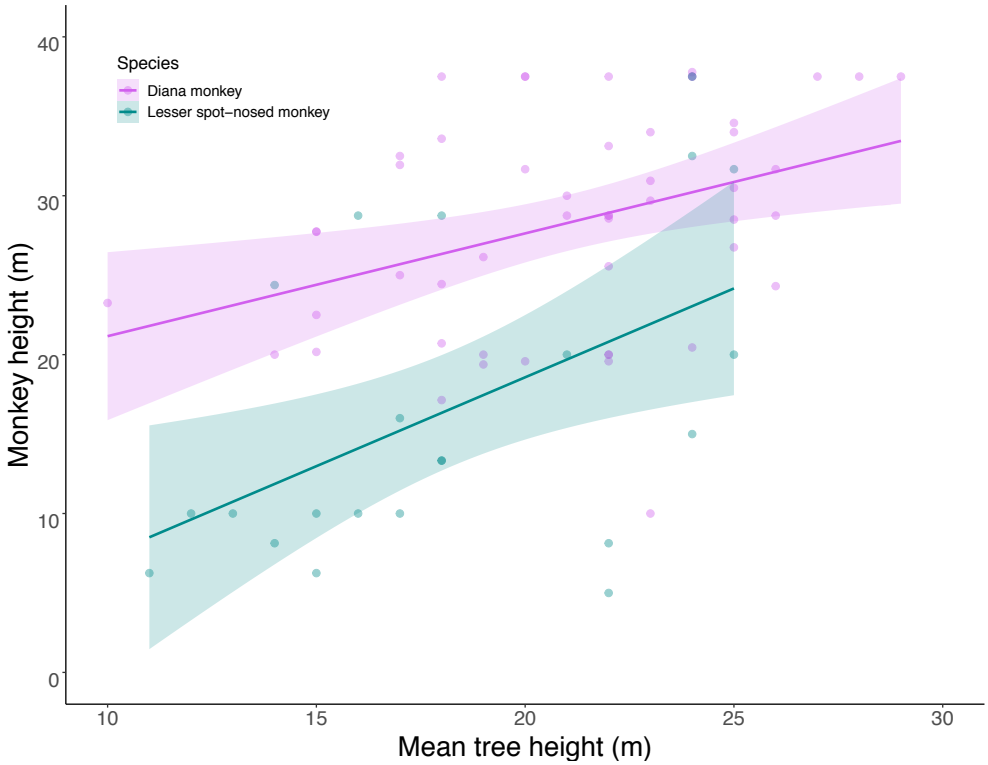

Figure 4.2 Height in trees of Diana monkeys and lesser spot-nosed monkeys increases with mean tree height. Line represents a glm with Gaussian error structure and 95% confidence intervals.

4.3.2.2 Lesser spot-nosed monkey

Mean lesser spot-nosed monkey height in trees across the study region was 16.59 metres ± SD 9.83. Variation in height in lesser spot-nosed monkeys was best explained by one hunting variable (law enforcement area) and one habitat variable (tree height) (Table 4.3). Law enforcement area was a strong

predictor of monkey height (AIC weight =1), with height lowest in the community forest (mean = 12.65; 95% CI: 6.44 to 18.85) and increasing by 0.37 metres and 11.87 metres in the GFNP (95% CI: -7.77 to 8.51) and in the GRNP (95% CI: 3.05 to 20.68) respectively (Figure 4.3b). Mean tree height was also a strong predictor of monkey height (AIC weight =1), with the height of lesser spot-nosed monkeys increasing by 0.83 metres (95% CI: 0.08 to 1.58) for every metre increase in mean tree height (Figure 4.2).

4.3.3 Visibility

4.3.3.1 Diana monkey

Mean visibility (visible monkey body parts divided by group size) of Diana monkeys before detection across the study region was 0.69 ± SD 0.44. Variation in visibility before detection was best explained by four predictors (Table 4.2): two hunting variables (law enforcement area and distance to settlements), one habitat variable (undergrowth visibility) and one group variable (number of species). Law enforcement area was not a good predictor of visibility (AIC weight =0.21). Visibility was lowest in the community forest (mean = 0.64; 95% CI: 0.40 to 0.88) and increased by 0.08 and 0.06 in the GFNP (95% CI: -0.25 to 0.41) and in the GRNP (95% CI: -0.21 to 0.33) respectively (Figure 4.3c). Distance to settlements (parameter estimate: -0.99; 95% CI: -2.45 to 0.46, AIC weight = 0.79), was a strongly supported variable but the direction of the effect depended on the other variables included in the model. Undergrowth visibility (parameter estimate: -0.00; 95% CI: -0.01 to 0.01, AIC weight = 0.17) and number of species (parameter estimate: 0.01;

95% CI: -0.07 to 0.08, AIC weight =0.17) were not good predictors of Diana monkey visibility.

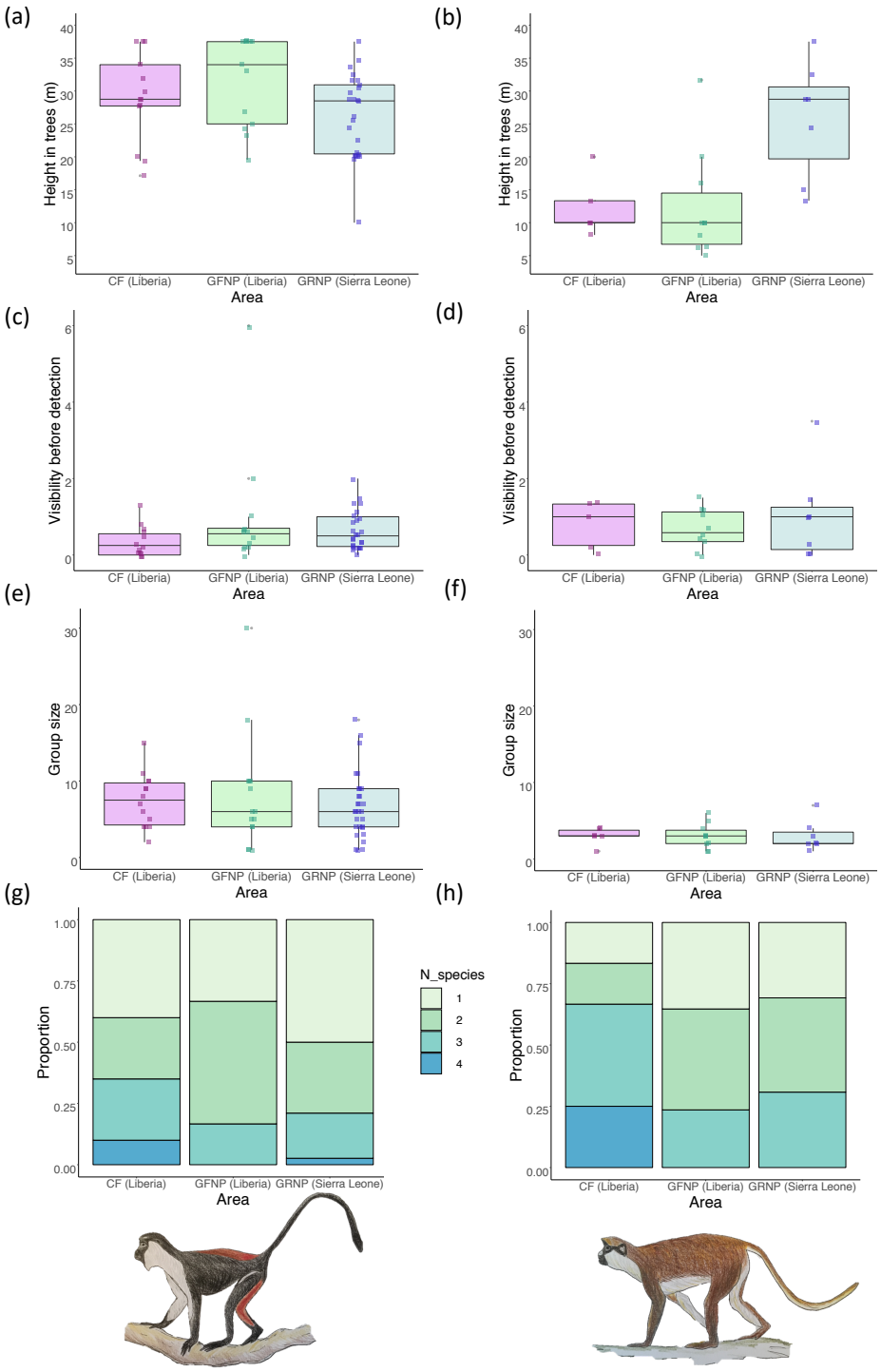

Figure 4.3 Differences in height in trees (a-b), visibility before detection (c-d), group size (e-f) and number of species in a group (g-h) of Diana monkeys (left) and lesser spot-nosed monkeys (right) between law enforcement areas. Box plots show first quartile, median and third quartile, vertical lines show ranges excluding outliers, dots show the raw data

4.3.3.2 Lesser spot-nosed monkey

Mean visibility of lesser spot-nosed monkeys before detection across the study region was 0.75 ± SD 0.51. Variation in visibility before detection was best explained by four predictors (Table 4.3), though none of the variables were strongly supported predictors of change in visibility: distance to settlements (parameter estimate: 0.20; 95% CI: -1.19 to 1.60, AIC weight = 0.15), tree height (parameter estimate: -0.01; 95% CI: -0.04 to 0.03, AIC weight = 0.19), undergrowth (parameter estimate: -0.00; 95% CI: -0.01 to 0.01, AIC weight = 0.18) and number of species (parameter estimate: -0.02; 95% CI: -0.16 to 0.12, AIC weight = 0.17). The null model was present in the top models (AIC weight =0.32), suggesting none of the included variables are good predictors of visibility before detection in lesser spot-nosed monkeys. Law enforcement area was not present as a predictor in the top models (Figure 4.3d).

4.3.5 Vocalisation

4.3.5.1 Diana monkey

Mean Diana monkey overall calls per minute across the study region was 2.54 ± SD 3.11. Variation in baseline vocalisations was best explained by three predictor variables (Table 4.2): two hunting variables (law enforcement area and distance to settlements) and one group variable (group size).

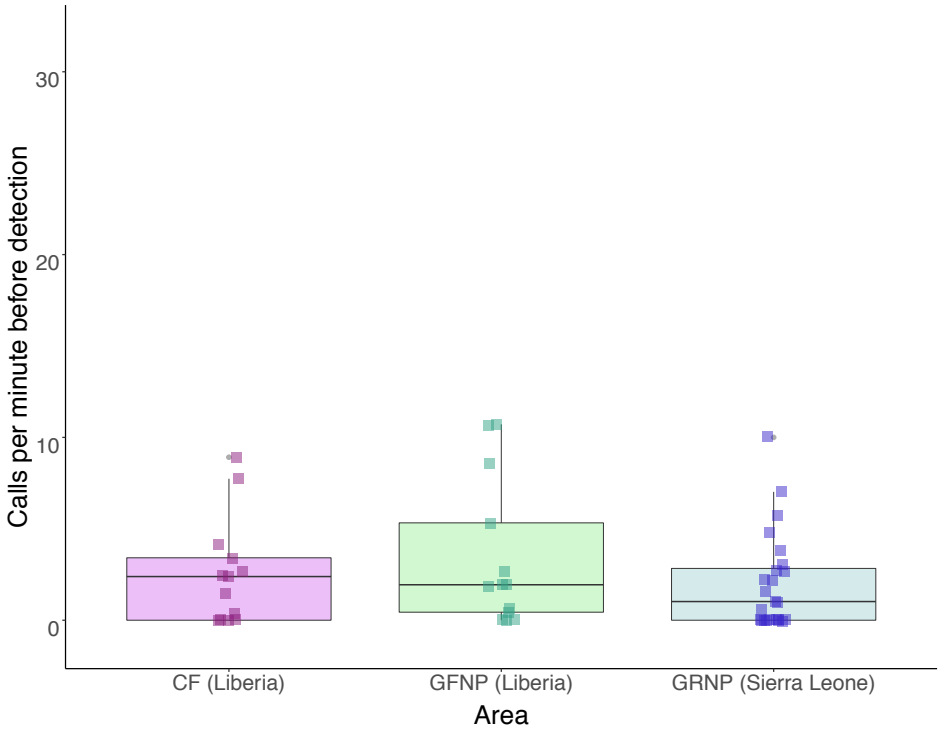

Figure 4.4 Diana monkey baseline vocalisation levels across law enforcement areas. Box plots show first quartile, median and third quartile, vertical lines show ranges excluding outliers, dots show the raw data

Law enforcement area was not a strongly supported predictor of baseline vocalisation (AIC weight = 0.22): calls per minute were intermediate in the community forest (mean = 2.52; 95% CI: 1.50 to 3.54), increased by 0.26 in the GFNP (95% CI: -1.17 to 1.69) and decreased by 0.10 in the GRNP (95% CI: -1.10 to 0.90) (Figure 4.4). Group size was a strong predictor of baseline vocalisation (AIC weight = 1), with an increase of 0.30 calls per minute with every additional individual present (95% CI: 0.10 to 0.50) (Figure 4.5). Distance to settlements (parameter estimate: -0.60; 95% CI: -5.01 to 3.82, AIC weight = 0.22) was not a strongly supported predictor of baseline vocalisation.

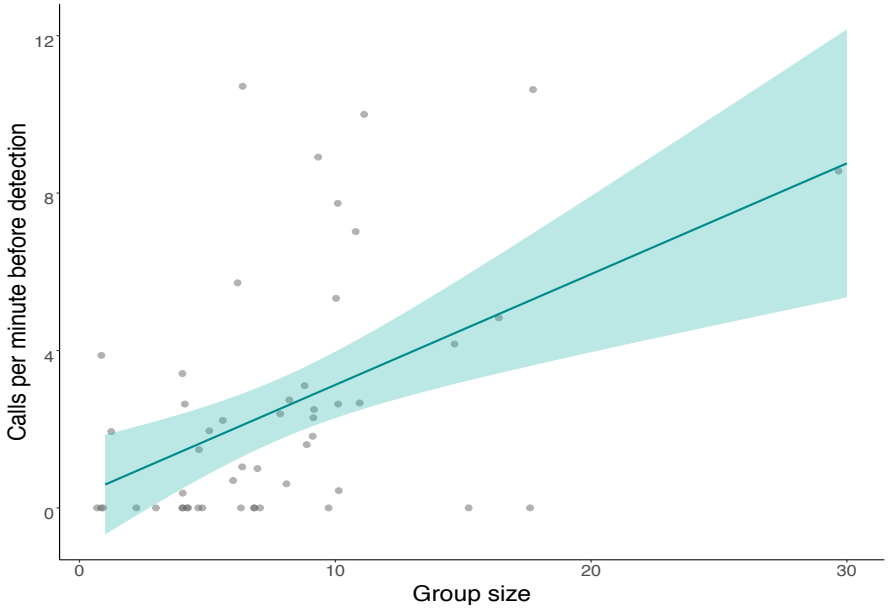

Figure 4.5 Number of calls per minute in Diana monkeys increases with group size. Line represents a glm with a Guassian error structure and 95% confidence intervals

4.3.1 Group size

4.3.1.1 Diana monkey

Mean group size of Diana monkeys across the study region was 7.24 ± SD 5.13. Variation in Diana monkey group size was best explained by one hunting variable (encounter rate of hunting signs) and one habitat variable (tree height) (Table 4.2). Encounter rate of hunting signs (Figure 4.6), was a strong predictor of group size (AIC weight = 1), with group size decreasing by 0.36 individuals with every 0.1 increase in hunting signs per km (95% CI: -0.69 to -0.02). Tree height was not a good predictor of group size (parameter estimate: -0.01; 95% CI: -0.04 to 0.02, AIC weight = 0.35). Law enforcement area was not present as a predictor in the top models (Figure 4.3e).

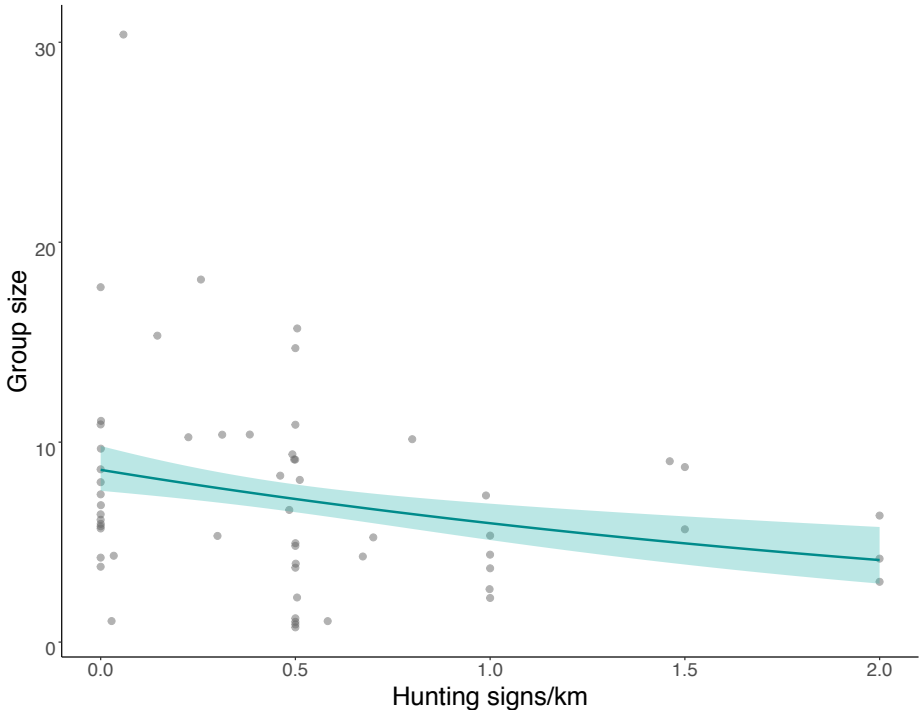

Figure 4.6 Group size of Diana monkeys decreases with an increase in hunting signs per km. Line represents a glm with Poisson error structure and 95% confidence intervals.

4.3.1.2 Lesser spot-nosed monkey

Mean group size of lesser spot-nosed monkeys across the study region was 3 ± SD 1.57. Variation in lesser spot-nosed monkey group size was best explained by one hunting variable (distance to settlements) and one habitat variable (undergrowth visibility) (Table 4.3). Neither distance to settlements (parameter estimate: 0.24; 95% CI: -1.42 to 1.90, AIC weight = 0.22) nor undergrowth visibility (parameter estimate: -0.002; 95% CI: -0.01 to 0.01, AIC weight =0.23) were good predictors of group size. The null model (AIC weight = 0.55) was present in the top models (Table 4.3), suggesting none of the included variables are good predictors of group size in lesser spot-nosed

monkeys. Law enforcement area was not present as a predictor in the top models (Figure 4.3f).

4.3.4 Number of species

4.3.4.1 Diana monkey

Across the study region, mean number of species present in a group in which Diana monkeys were present was 1.84 ± SD 0.88. Variation in number of species present in each group was best explained by habitat variables tree height and undergrowth visibility (Table 4.2). None of the hunting predictor variables, including law enforcement area (Figure 4.3g) were present as predictors of number of species in a group. Neither tree height (parameter estimate: 0.97; 95% CI: 0.95 to 1.04, AIC weight = 0.22), nor undergrowth visibility (parameter estimate: 0.99; 95% CI: 0.98 to 1.02, AIC weight = 0.23) were good predictors of number of species. The null model was present in the top models (AIC weight =0.55), suggesting none of the included variables are good predictors of number of species in a group.

4.3.4.2 Lesser spot-nosed monkey

Across the study region, mean number of species present in a group in which lesser spot-nosed monkeys were present was 2.17 ± SD 0.94. Variation in number of species present in each group was best explained by four predictors (Table 4.3): two hunting variables (law enforcement area and encounter rate of hunting signs), one habitat variable (tree height) and one resource variable

(presence of fruit). None of the variables, however, were very strong predictors of number of species in a group. Law enforcement area was a fairly strong predictor of number of species (AIC weight = 0.64) but the direction of the effect depended on the other variables included in the model. Number of species present was highest in the community forest with the odds of an increase in number of species 85% and 80% lower in the GFNP (95% CI: 0.03 to 2.64) and in the GRNP (95% CI: 0.05 to 2.68) respectively (Figure 4.3h). Encounter rate of hunting signs (parameter estimate: 2.05; 95% CI: 0.61 to 1.93, AIC weight = 0.11), tree height (parameter estimate: 1.09; 95% CI: 0.93 to 1.12, AIC weight = 0.22) and presence of fruit (parameter estimate: 3.06 95% CI: 0.43 to 8.26, AIC weight = 0.56) were not strongly supported predictors of number of species. The null model was also present in the top models (AIC weight =0.08).

Table 4.2 Top candidate models exploring change in Diana monkey baseline behaviour

Response	model	k	AICc	ΔAICc	weight
Monkey height	height	3	338.80	0.00	0.30
	height + area	5	338.82	0.03	0.30
	height + undergrowth	4	340.26	1.46	0.15
	height + undergrowth + area	6	340.50	1.71	0.13
	height + distance	4	340.64	1.85	0.12
Visibility before detection	distance	3	61.18	0.00	0.45
	area	4	62.67	1.48	0.21
	undergrowth + distance	4	63.17	1.98	0.17
	n.species + distance	4	63.17	1.99	0.17
Vocalisation before detection	group size	3	252.16	0.00	0.56
	group size + area	5	254.04	1.88	0.22
	group size + distance	4	254.05	1.89	0.22
Group size	signs	3	334.20	0.00	0.65
	height + signs	4	335.47	1.26	0.35
Number of species	null	3	185.06	0.00	0.55
	undergrowth	4	186.81	1.75	0.23
	height	4	186.93	1.87	0.22

***** area = law enforcement area, distance = distance to settlements, signs = encounter rate of hunting signs, height = mean tree height, undergrowth = undergrowth visibility, group size = number of monkeys in a group, n.species = number of species present, null = null model

Table 4.3 Top candidate models exploring change in lesser spot-nosed monkey baseline behaviour

Response	model	k	AICc	ΔAICc	weight
Monkey height	height + area	5	157.83	0.00	1
Visibility before detection	null	2	36.57	0.00	0.32
	height	3	37.64	1.07	0.19
	undergrowth	3	37.75	1.18	0.18
	n.species	3	37.83	1.26	0.17
	distance	3	38.08	1.52	0.15
Group size	null	1	85.81	0.00	0.55
	undergrowth	2	87.57	1.76	0.23
	distance	2	87.64	1.84	0.22
Number of species	area	5	111.81	0.00	0.21
	fruit + area	6	111.86	0.04	0.21
	fruit	4	112.36	0.54	0.16
	height + area	6	112.67	0.85	0.14
	fruit + signs	5	113.11	1.29	0.11
	fruit + height + area	7	113.71	1.90	0.08
	null	3	113.78	1.97	0.08

***** area = law enforcement area, distance = distance to settlements, signs = encounter rate of hunting signs, height = mean tree height, undergrowth = undergrowth visibility, fruit = presence of fruit, n.species = number of species present, null = null model

4.4 Discussion

The aim of this chapter was to determine the effect that variation in human hunting pressure may have on baseline antipredator defences of Diana monkeys and lesser spot-nosed monkeys. Both species were expected to exhibit more cryptic behaviours where the pressure from human hunting was higher, with Diana monkeys showing stronger responses given their higher vulnerability to hunting compared to lesser spot-nosed monkeys. Overall, neither Diana monkeys nor lesser spot-nosed monkeys displayed major differences in baseline defences in response to varying hunting pressure. Group size in Diana monkeys, however, decreased with an increase in encounter rate of hunting signs, in line with the expectation of a stronger response in this species.

A number of studies have observed changes in prey use of canopy strata associated with the type of predator (Vanderwerf 2012; Coleman and Hill 2014). Results from this study, however, indicate that height in trees in Diana monkeys was not affected by hunting pressure at our study site. Similarly, height of woolly monkeys, *Lagothrix poeppigii*, did not differ between a high and a low hunting pressure site in Ecuador (Papworth et al. 2013). Lesser spot-nosed monkeys were found significantly higher up in trees in the GRNP in Sierra Leone compared to both regions in Liberia. This result is surprising, since hunting pressure in the GRNP is expected to be the lowest across the study region. It is possible that other pressures, such as the presence of other predators and the availability of food, may be affecting lesser spot-nosed

monkey's height in trees in the GRNP. McGraw (2000) highlights how lesser spot-nosed monkeys tend to use the understory more often and move across lower branches, as the undergrowth provides more food and a good refuge for the species (Buzzard 2006). At both sites in Liberia, height of lesser spot-nosed monkeys reflects understory strata use, suggesting perhaps the benefits of foraging and travelling at their preferred height outweigh the cost of predation. McGraw's study also shows lower overall average heights for Diana monkeys in Taï National Park (McGraw 2000) compared to the ones recorded in this study, suggesting an overall preference of this species for higher strata in Gola. Furthermore, in this study tree height was a strong predictor of monkey height in trees, further supporting a preference for higher canopy where available. This could be linked to overall higher hunting pressure across the Gola region compared to other locations. A study on Diana monkeys found they used higher strata in the presence of humans in a hunted area compared to an unhunted area, however, as the height before the monkeys detect the human observers is not recorded, it is not clear whether there is an increase in strata use following detection (Koné and Refisch 2007).

When the pressure from predation is high, many animals seek shelter and concealment in dense habitat. This has been observed, for example, in red deer, *C. elaphus*, at the onset of the hunting season (Lone et al. 2015). Primates have been found to both avoid areas of low visibility to allow clearer views of predators as well as spend more time in dense foliage to seek cover from predators (Emerson et al. 2011; Coleman and Hill 2014). The results from this study, however, found no difference in the visibility of monkeys as

a result of varying hunting pressure in either species. Visibility of both species was very low across the region, suggesting a preference to hide behind thick foliage. Although not significant, Diana monkeys did show lower visibility in the community forest which reflects expectations, as this is likely one of the areas with higher hunting pressure.

Contrary to predictions, baseline vocalisation levels in Diana monkeys did not change with intensity of hunting pressure. This result supports data from Taï National Park in Ivory Coast where no differences in Diana monkey calls prior to playbacks were recorded between a hunted and an unhunted site (Bshary 2001). Baseline calls per minute in this study, however, were fewer compared to those in Taï National Park, suggesting perhaps higher overall pressure from hunting in Gola but also likely because group sizes were smaller in Gola compared to Taï National Park. Perhaps unsurprisingly, group size was a strong predictor of call frequency, with bigger groups significantly more vocal than smaller ones. This pattern is likely linked to more individuals producing more calls overall and to an increased level of vocal communication in bigger groups.

For Diana monkeys, the results of this study are consistent with previous studies in snub-nosed langurs, *S. concolor*, and white-fronted spider monkeys, *Ateles belzebuth*, which both recorded smaller group sizes associated with increased human hunting pressure (Watanabe 1981; Aquino et al. 2013). Here, an increasing number of hunting signs per km was associated with a smaller group size in Diana monkeys, suggesting that

monkeys may be reducing group size to avoid being detected by hunters. Another explanation is that increased hunting pressure is reducing overall densities and consequently affecting group size. In contrast, no difference in group size associated with hunting pressure was found in lesser-spot nosed monkeys. Furthermore, none of the other hunting variables predicted changes in group size in Diana monkeys. This reflects studies on other *Cercopithecus* monkeys which found no relationship between hunting and group size in field sites in Gabon and Equatorial Guinea (Croes et al. 2006; Kümpel et al. 2008). These studies both compare overall differences between sites (similar to the law enforcement area predictor in this study) rather than fine scale differences such as those captured by encounter rate of hunting signs. Perhaps then, group size is reduced locally in response to specific hunting events and not in a way that is detectable across large areas. These contrasting results may also be linked to the multiple factors that influence group size, which include other predators and the distribution of food (Janson and Goldsmith 1995).

Mean group size for both species across the study region was considerably lower than that reported in other studies on Diana monkeys and lesser spot-nosed monkeys on Tiwai Island in Sierra Leone and in Taï National Park in Ivory Coast (Oates et al. 1990; Zuberbühler and Jenny 2002). This could be a reflection of general overall higher hunting intensity in Gola but is likely due to the extreme difficulty in getting accurate group size estimates in dense tropical forests. Since reported numbers are based on number of observed individuals, it is very likely that these are underestimates of true group size in the study region.

Consistent with findings by Croes et al. (2006), this study does not find a change in proportion of polyspecific groups with hunting pressure in either species. Across the whole study region, polyspecific groups were prevalent, suggesting clear benefits for maintaining polyspecific associations despite human hunting pressure, such as increased foraging efficiency and predator avoidance (Gautier-Hion et al. 1983; Bshary and Noë 1997b).

Overall most of the baseline defences for both species did not change with human hunting pressure, but behaviours were generally more cryptic across the study region compared to other studies on the same species. Perhaps human hunting pressure is too recent to have strong evolutionary significance (Zuberbühler and Jenny 2002) and therefore prey behavioural patterns vary considerably between sites/studies. However, given the highly efficient hunting strategies adopted by humans and how quickly animals respond to fluctuating risk (Lima and Bednekoff 1999), changes in behavioural patterns linked to hunting would likely be consistent. It could be that despite differences in law enforcement and measured variation in hunting intensity across the study region, monkeys still perceive humans as a threat throughout. Park patrols in the GRNP could potentially have an effect on perceived predation risk, since the enforcement change occurred only in recent years. Furthermore, despite clear variation in hunting intensity, hunting does still occur throughout the study region, with no area completely unhunted. Future work investigating variation in behaviour linked to hunting would benefit from including a truly unhunted area. Having a "control" treatment area would help to discern the potential variation in behaviour more clearly. The

core zones of some protected areas in Gabon and the Republic of Congo, for example, are truly unhunted and could function as an ideal control treatment area to investigate this further.

An alternative explanation is that monkeys are not adapting their baseline defences to human hunting pressure and other factors are driving observed patterns in Gola. There are likely many factors influencing the behaviour of these species and in order to gain a true understanding of the drivers and how they interact, data on the distribution of other predators should be collected. This data unfortunately is hard to collect, given the low abundance of predators such as chimpanzees and leopards in Gola (Klop et al. 2008.).

Perhaps baseline adaptations have indeed developed but are too costly for prey species to maintain for prolonged periods of time. According to the 'predation risk allocation hypothesis' prey will adjust their antipredator behaviours according to the temporal variation in risk (Lima and Bednekoff 1999). Species, however, will decrease antipredator behaviour effort under prolonged high risk situations, as the cost of a sustained reduction in time allocated to foraging and other fitness enhancing activities, outweighs the benefits derived from a constant antipredator strategy (Lima and Bednekoff 1999). Given the high pressure from hunting in Gola, perhaps neither species can afford to constantly adopt baseline antipredator defences against humans.

It was surprising that the gunshot frequency map was not a strong predictor of behavioural change. An alternative explanation is that the hunting

predictors used in this study are not capturing localised risk history in these species. As baseline behaviours are a product of an animal's experiences, current perception of risk and consequent behaviours are a result of a cumulative change in hunting pressure patterns. A static measure of hunting may be unable to capture these patterns.

Overall, baseline defences are costly to sustain, as in order to be effective they need to be maintained for prolonged periods of time under the risk of a potential threat. On the other hand, immediate risk (i.e. predator presence) inevitably poses a strong pressure on prey to act accordingly and thus the presence of a predator is expected to elicit stronger responses where that predator is perceived as a greater risk. In the next chapter the potential relationships between secondary/reaction defences and hunting pressure are explored.

Chapter 5

Does hunting affect the reaction behaviour of Diana monkeys, *Cercopithecus diana*, and lesser spot-nosed monkeys, *Cercopithecus petaurista*?

5.1 Introduction

The previous chapter focussed on baseline defences that animals adopt to minimise the chances of encountering or being detected by a predator. Once in the presence of a predator, prey can further respond in a variety of ways to increase the likelihood of survival. These behavioural adaptations are termed secondary/reaction defences (Edmunds 1974). Examples of these include fleeing, freezing/hiding, which are avoidance behaviours that aim at reducing confrontation with the predator, as well as vocalising, inspecting and mobbing, which are deterrent behaviours that tend to discourage, intimidate and confuse the predator (Lima and Dill 1990; Caro 2005). Again, as humans are pursuit predators, prey are likely to adopt avoidance reaction defences against hunters, in contrast with reactions to ambush predators (i.e. leopards) which rely on signalling detection. Furthermore, in accordance with risk perception theories (i.e. the Landscape of Fear), a species forms a mental map based on their perception of spatial variation in risk and thus prey is likely to

develop stronger responses in areas of higher risk compared to areas where predation pressure is low (Laundré et al. 2010).

By increasing fleeing distance from a predator, prey reduce the chance of being detected or attacked by that predator (Broom and Ruxton 2005). As fleeing is costly, however, prey are likely to flee earlier under conditions of higher threat and reduce fleeing distance when the cost of predation is low, as this may allow animals longer feeding time for example (Broom and Ruxton 2005; Stankowich and Blumstein 2005). Flight initiation distance (FID), the distance at which animals flee at the approach of the observer, varies with predation pressure and can be used as a measure of perceived predation risk (Ydenberg and Dill 1986; Mikula et al. 2018). In many bird species, for example, FID doubles in the presence of nests of predatory hawks, *Accipiter nisus* and *A. gentilis* (Møller et al. 2017). Similar patterns have been found as a result of human predation in both ungulates and birds. Both impala, *Aepyceros melampus*, and greater kudu, *Tragelaphus strepsiceros*, show increased FID in hunted areas compared to a protected area in Zimbabwe (Tarakini et al. 2014). Ostriches, *Struthio camelus*, have longer FIDs within the partially protected areas outside compared to within the Serengeti National Park (Magige et al. 2009). Although FID provides a good indication of the perceived level of threat of an animal, what occurs following the initial fleeing response also provides a useful indication of perceived predation risk (Tätte et al. 2018). Under high risk, prey may not only flee at a larger distance but may also flee faster once detected. Birds in a rural landscape, for example, fled further compared to ones in an urban environment in Estonia (Tätte et al. 2018).

Alternatively, freezing and immobilisation defences function by decreasing the conspicuousness of prey species (Caro 2005). Adopting a state of complete immobility under high risk situations, in fact, may decrease the likelihood of detection and is often adopted as an immediate response triggered by the detection of a predator (Chelini et al. 2009). The adoption of freezing behaviour (vs fleeing) is highly context dependant and may vary depending on many factors, including detection distance, the predator and the type of habitat (Eilam 2005). Many forest dwelling ungulates, for example, adopt freezing antipredator behaviours, given the high coverage provided by a forest habitat (Takada et al. 2018). The freezing response has been recorded as a reaction to human hunting pressure. The black colobus, *Colobus satanas,* preferred prey by hunters in continental Equatorial Guinea, showed an increase in freezing behaviour in areas with high levels of human hunting (Kümpel et al. 2008). In contrast, duiker species in southwestern Gabon rapidly fled from humans in areas with high levels of hunting and remained stationary in an area of no hunting (Croes et al. 2006).

Some prey may actually inspect a potential predator upon encounter (Lima and Dill 1990). Inspection is a response that serves primarily for predator recognition and to gain information on predator state (Lima and Dill 1990). As this is highly risky behaviour, probability of inspection is likely to decrease with increasing risk. Inspection probability in European minnows, *Phoxinus phoxinus*, for example, is inversely related to their perception of risk (Magurran and Girling 1986). In contrast, Diana monkeys, *Cercopithecus diana,* show strong inspection behaviour in the presence of humans in both a

hunted and a unhunted area in Taï National Park, Ivory Coast (Koné and Refisch 2007).

After detecting a predator, prey may vocalise to signal presence to conspecifics, but may also be signalling detection to the predator (Caro 2005). This type of antipredator strategy, in fact, works best against ambush predators, as the vocalisation signals to the predator that it has been detected, reducing probability of attack. Prey have developed a very complex suite of antipredator alarm calls. For example, different types of alarm calls specific to different predators have been recorded in vervet, *Cercopithecus aethiops*, Campbell's, *C. campbelli*, and Diana monkeys (Struhsaker 1967; Zuberbühler et al. 1997; Zuberbühler 2001). Species may also adapt their call rate depending on the predator (Caro 2005). North American pikas, *Ochotona princeps*, for example, reduced call rate in response to weasels compared to martens, since weasels represent a bigger threat as they can follow the animals within the rock burrows (Ivins and Smith 1983). Songbirds are less likely to sing at dawn in areas where recordings of predator calls are played (Santema et al. 2019). Similarly, a reduction in vocalisation levels is expected as a reaction to human presence (Zuberbühler et al. 1997; Bshary 2001; Dooley and Judge 2015). Diana monkeys in Taï National Park, for instance, did not sound alarm calls in response to human hunters (Zuberbühler et al. 1997) and have been shown not to respond to human imitations of predator calls (Bshary 2001), thus suggesting adaptive discrimination abilities of this species in response to humans. This adaptation was not as pronounced in regions with lower levels of hunting, suggesting a strong learning component and

association of humans as predators in regions with high levels of hunting and risk.

As highlighted above, variation in predator type and predation risk can have strong effects on the reaction defences of prey species. These reaction behaviours may also have an impact on fitness, as species will generally be diverting time otherwise invested in activities that would benefit their fitness (i.e. foraging and feeding, searching for mates, resting). Research at the interface between antipredator behaviours and unsustainable exploitation of wildlife by 'human predators' is limited (Berger-Tal et al. 2016). This chapter explores spatial variation in reaction defences of Diana monkeys and lesser spot-nosed monkeys as a result of varying levels of hunting pressure measured using different methods detailed in Chapter 3. The recorded behaviours were flight initiation distance, fleeing time, visibility, vocalisation levels and inspection behaviour. Monkey behavioural responses are expected to vary as follows:

1. Flight initiation distance is expected to be longer in areas with higher hunting pressure
2. Time till fleeing is expected to be shorter in areas with higher hunting pressure
3. Visibility, calling and inspection behaviour are expected to be lower in areas with higher hunting pressure
4. Behavioural differences related to hunting are expected to be more pronounced in Diana monkeys compared to lesser spot-nosed monkeys

5.2 Methods

For details on study site, study species, behavioural data collection and analysis see Chapter 2.

5.2.1 Statistical Analysis

The covariates added to each model, alongside reasons for inclusion, are listed in Table 5.1. The predictor variable group size was log transformed to reduce spread and improve model fit. Flight initiation distance (FID) was modelled using linear models with a Gaussian error structure.

Fleeing time, which is defined as the time it takes a group to be completely out of sight following detection, was treated as a count variable, as the data was rounded up to the closest minute and does not contain negative values. Due to overdispersion of data in a GLM with Poisson error structure, fleeing time was modelled using a GLM with a negative binomial error structure.

Analysis on change in visibility was conducted only with observations for which data on visibility both before and after detection was available (Diana monkeys: n=51; lesser spot-nosed monkeys: n=22). Change in visibility is defined as the number of visible body parts before detection minus the number of visible body parts following detection, divided by group size. Change in visibility was modelled using linear models with a Gaussian error structure.

Probability of inspection was investigated by grouping the six reaction categories (Table 2.2) into one category for ‘inspection’ and one category for

'no inspection'. Inspection probability was then modelled using a binary logistic regression.

Analysis on change in calls per minute was conducted only with observations for which recordings of both before and after detection were available (Diana monkeys: n=50). Change in calls per minute is defined as the number of calls per minute before detection minus the number of calls per minute following detection. Both change in alarm calls and change contact calls were modelled using linear models with a Gaussian error structure.

Gunshot frequency was only present as a predictor in top models for change in visibility and probability of inspection in Diana monkeys. For change in visibility, both law enforcement area and gunshot frequency were present in top models; these predictors are collinear hence for this case model averaging was not carried out and this analysis was not included in the thesis. For probability of inspection, plotted residuals showed poor model fit, therefore only results from the complete dataset (i.e. not reduced for comparison with the gunshot frequency map) were included using the three predictors of hunting intensity which were available across the study area: law enforcement area, distance to settlements and encounter rate of hunting signs.

Parameter estimates and confidence intervals were derived from full model averaging of top models with $\Delta AICc \leq 2$. If a single best model was selected, then parameter estimates and confidence intervals from this model were reported. Reported mean estimates of different behavioural responses in the community forest (intercept) were derived from the averaged model, with all other variables held at an average.

Table 5.1 List of confounding variables selected to predict specific reaction behaviours in Diana monkeys and lesser spot-nosed monkeys in Gola

Response	Variable type	Variable	Reason for inclusion in model
Flight initiation distance	Habitat variables	Mean tree height	Higher trees likely increase monkey's starting height which increases monkey-observer starting distance
		Undergrowth visibility	Reduced visibility can influence detectability distance
	Resource variables	Fruit presence	Presence of fruit may deter fleeing
	Monkey variables	Group size	Lower perceived risk in larger groups may reduce fleeing distance, increased vigilance in larger groups may increase fleeing distance
		Number of species	Lower perceived risk in polyspecific groups may reduce fleeing distance, increased vigilance in polyspecific groups may increase fleeing distance
Time till fleeing	Resource variables	Fruit presence	Presence of fruit may deter fleeing
	Monkey variables	Group size	Lower perceived risk in larger groups may increase fleeing time; also more individuals likely take longer to flee
		Number of species	Lower perceived risk in poly-specific groups may increase fleeing time
Change in visibility	Monkey variables	Number of species	Lower perceived risk in polyspecific groups may reduce probability of hiding
Inspection	Habitat variables	Mean tree height	Higher trees likely reduce observer's detection of inspecting behaviour; also may decrease monkey's perceived risk as monkeys are further away
		Undergrowth visibility	Reduced visibility likely reduces observer's detection of inspecting behaviour
	Monkey variables	Group size	Lower perceived risk in larger groups may increase probability of inspection
		Number of species	Lower perceived risk in polyspecific groups may increase probability of inspection
Change in vocalisation	Habitat variables	Mean tree height	Higher trees may reduce monkey's perceived risk as monkeys are further away from observer
		Undergrowth visibility	Reduced visibility may reduce monkey's perceived risk
	Monkey variables	Group size	Larger groups are likely more vocal
		Number of species	Number of species likely influences vocalization levels
		Reaction distance	Distance at which monkeys detect the observer likely influences vocalisation levels

5.3 Results

For details on survey effort and number of observations see Chapter 4 (*4.3 Results*).

5.3.1 Flight initiation distance (FID)

5.3.1.1 Diana monkey

Mean FID of Diana monkeys across the study region was 31.38 metres ± SD 10.98. Variation in FID was best explained by four predictors (Table 5.2): one hunting variable (law enforcement area), two habitat variables (tree height and undergrowth visibility) and one group variable (number of species). Law enforcement area was a strong predictor of FID (AIC weight = 1.00), with FIDs the greatest in the community forest (mean = 36.70; 95% CI: 31.02 to 42.37) and reducing by 6.40 metres and 8.28 metres in the GFNP (95% CI: -13.92 to 1.13) and in the GRNP (95% CI: -14.85 to -1.70) respectively (Figure 5.1a). Tree height was the only other significant predictor of FID (AIC weight = 1.00), with FID increasing by 0.94 metres (95% CI: 0.28 to 1.60), for every metre increase in mean tree height. Number of species (parameter estimate: 0.84; 95% CI: -2.29 to 3.96) and undergrowth visibility (parameter estimate: 0.05; 95% CI: -0.15 to 0.26) were both present in two of the averaged models (Table 5.2) but were not strongly supported predictors of FID (AIC weights = 0.38 and 0.36 respectively).

5.3.1.2 Lesser spot-nosed monkey

Mean FID of lesser spot-nosed monkeys across the study region was 30.65 metres ± SD 12.31. Variation in FID was best explained by six predictors (Table 5.3): two hunting variables (law enforcement area and distance to settlements), one habitat variable (tree height), two group variables (number of species and group size) and one resource variable (presence of fruit). Law enforcement area was a strong predictor of FID (AIC weight = 0.90), with FIDs the greatest in the community forest (mean = 48.14; 95% CI: 32.85 to 63.44) and reducing by 18.26 metres and 18.39 metres in the GFNP (95% CI: -34.52 to -2.00) and in the GRNP (95% CI: -35.37 to -1.41) respectively (Figure 5.1b). Number of species (parameter estimate: -5.93; 95% CI: -12.75 to 0.89, AIC weight = 0.90) and group size (parameter estimate: -13.77; 95% CI: -30.55 to 3.02, AIC weight = 0.88) were strongly supported variables but the direction of the effect depended on the other variables included in a model. All other variables were not strongly supported predictors of FID: distance to settlements (parameter estimate: 6.45; 95% CI: -34.91 to 47.81, AIC weight = 0.10), tree height (parameter estimate: 0.36; 95% CI: -0.71 to 1.43, AIC weight = 0.40) and presence of fruit (parameter estimate: 2.47; 95% CI: -8.71 to 13.65, AIC weight = 0.22).

5.3.2 Fleeing time

5.3.2.1 Diana monkey

Mean Diana monkey fleeing time across the study region was 5.76 minutes ± SD 4.08. Variation in fleeing time was best explained by four predictors (Table 5.2): one hunting variable (law enforcement area), one resource variable (presence of fruit), and two group variables (group size and number of species). Law enforcement area was a strong predictor of fleeing time (AIC weight = 1), with fleeing time lowest in the community forest (mean = 3.83; 95% CI: 2.43 to 5.23) and increasing by 0.19 and 0.54 minutes in the GFNP (95% CI: -0.28 to 0.66) and in the GRNP (95% CI: 0.14 to 0.94) respectively (Figure 5.1c). Group size was also a strong predictor of fleeing time (AIC weight = 1), with fleeing time increasing with group size (parameter estimate:0.87; 95% CI: 0.47 to 1.26). Number of species (parameter estimate: -0.02; 95% CI: -0.14 to 0.11, AIC weight = 0.21) and presence of fruit (parameter estimate: 0.04; 95% CI: -0.17 to 0.26, AIC weight = 0.26) were both present in one of the averaged models (Table 5.2) but were not good predictors of fleeing time.

5.3.2.2 Lesser spot-nosed monkey

Mean lesser spot-nosed monkey fleeing time across the study region was 3.44 minutes ± SD 4.47. Variation in fleeing time was best explained by two group predictor variables (Table 5.3): group size and number of species. None of the hunting predictor variables, including law enforcement area (Figure 5.1d),

were present in the top models. Plotted residuals showed poor model fit, which could be due to the small sample size and to one observation causing a large outlier. Model results are included in the thesis despite poor model fit. Number of species present was a strong predictor of fleeing time (AIC weight = 1), with fleeing time increasing by 0.61 minutes for every additional species present (95% CI: 0.28 to 0.94). Group size was present in one of the averaged models (Table 5.3) but was not a good predictor of fleeing time (parameter estimate: 0.51; 95% CI: -0.83 to 1.83, AIC weight = 0.5).

5.3.3 Change in visibility

5.3.3.1 Diana monkey

Mean change in visibility of Diana monkeys across the study region was 0.14 ± SD 0.72. Change in visibility was best explained by two hunting predictor variables (Table 5.2): law enforcement area and encounter rate of hunting signs. Law enforcement area was not a good predictor of change in visibility (AIC weight = 0.45). Change in visibility was intermediate in the community forest (mean = 0.06; 95% CI: -0.27 to 0.40), decreased by 0.05 in the GFNP (95% CI: -0.44 to 0.33) and increased by 0.16 in the GRNP (95% CI: -0.31 to 0.65) (Figure 5.1e). Encounter rate of hunting signs was also not a good predictor of change in visibility (parameter estimate: 0.03, 95% CI: -0.18 to 0.24, AIC weight = 0.17). The null model (AIC weight = 0.38) was present in the top models (Table 5.2), suggesting none of the hunting variables are good predictors of change in visibility in Diana monkeys.

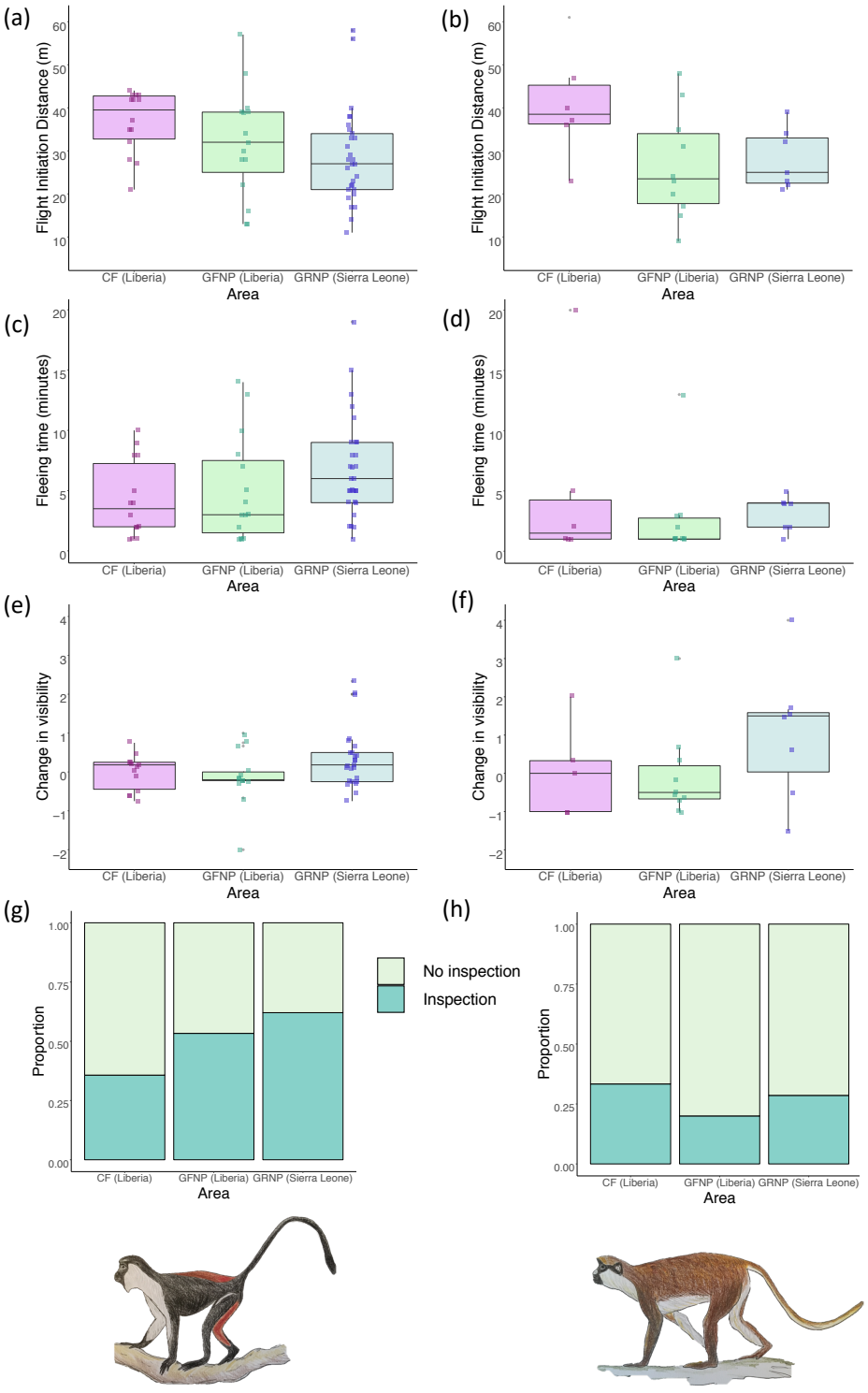

Figure 5.1 Differences in flight initiation distance (a-b), fleeing time (c-d), visibility change (e-f) and inspection (g-h) of Diana monkeys (left) and lesser spot-nosed monkeys (right) between law enforcement areas. Box plots show first quartile, median and third quartile, vertical lines show ranges excluding outliers, dots show the raw data

5.3.3.2 Lesser spot-nosed monkey

Mean change in visibility of lesser spot-nosed monkeys across the study region was 0.32 ± SD 1.43. Change in visibility was best explained by one hunting variable (law enforcement area) and one group variable (number of species) (Table 5.3). Law enforcement was a strong predictor of change in visibility (AIC weight = 1), with change in visibility smallest in the community forest (mean = -1.29; 95% CI: -2.58 to -0.01) and increasing by 1.24 and 2.40 in the GFNP (95% CI: -0.34 to 2.81) and the GRNP (95% CI: 0.72 to 4.07) respectively (Figure 5.1f). Number of species was also a significant predictor of change in visibility (AIC weight = 1), with change in visibility increasing by 1.04 for every additional species present (95% CI: 0.38 to 1.71).

5.3.4 Inspection

5.3.4.1 Diana monkey

Following detection, Diana monkeys inspected the observers 54% of the time across the study region. Probability of inspection was best explained by four predictors (Table 5.2): one hunting variable (distance to settlements), two habitat variables (tree height and undergrowth visibility) and one group variable (group size). Group size was a strong predictor of inspection probability (AIC weight = 1), with every additional individual present increasing the odds of inspection by 1.62 (95% CI: 0.06 to 3.18) (Figure 5.2). Distance to settlements (parameter estimate = -5.27; 95% CI: -13.00 to 2.44,

AIC weight = 0.83), tree height (parameter estimate = 0.07; 95% CI: -0.09 to 0.23, AIC weight = 0.63) and undergrowth visibility (parameter estimate = -0.04; 95% CI: -0.11 to 0.03, AIC weight = 0.81) were supported predictors of inspection probability but the direction of the effect depended on the other variables included in a model. Law enforcement area was not present as a predictor in the top models (Figure 5.1g).

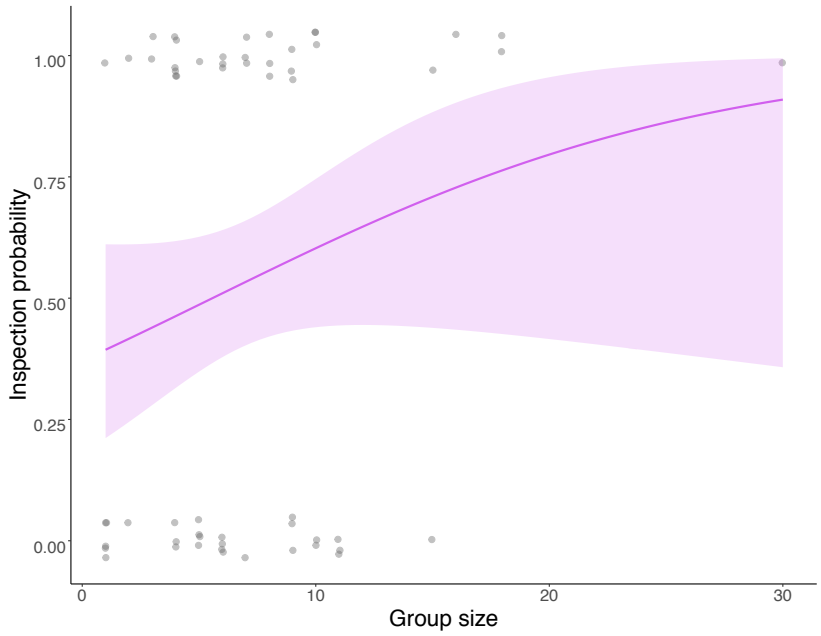

Figure 5.2 Probability of inspection in Diana monkeys increases with group size. Line represents a glm with a binomial error structure and 95% confidence intervals

5.3.4.2 Lesser spot-nosed monkey

Following detection, lesser spot-nosed monkeys inspected the observers 26% of the time across the study region. Plotted residuals showed poor model fit, which again could be due to the small sample size. Model results are included in the thesis despite poor model fit. Top models included one hunting variable (encounter rate of hunting signs) and one group variable (number of species) (Table 5.3). Neither encounter rate of hunting signs (parameter estimate: 1.78; 95% CI: -0.21 to 4.65, AIC weight = 0.81) or number of species (parameter

estimate: 0.43; 95% CI: -0.36 to 1.95, AIC weight =0.54) were good predictors of inspection probability. Law enforcement area was not present as a predictor in the top models (Figure 5.1h).

5.3.5 Vocalisation

5.3.5.1 Diana monkey

Overall, Diana monkeys produced 5.92 (95% CI: 4.08 to 7.76) more alarm calls per minute (paired t-test, t=6.46, df=50, p<0.001) and produced 1.57 (95% CI:-2.62 to -0.52) fewer contact calls per minute (paired t-test, t=-3.01, df=50, p=0.004) after detecting the observers compared to before detection (Figure 5.3a and 5.3b).

Change in alarm calls was best explained by five predictors (Table 5.2): two hunting variables (law enforcement area and distance to settlements), one habitat variable (tree height) and two group variables (group size and reaction distance). Law enforcement area was a fairly supported predictor of change in alarm call (AIC weight = 0.62) but the direction of the effect depended on the other variables included in a model: change in alarm calls was lowest in the community forest (mean = 3.75; 95% CI: -0.73 to 8.24) and increased by 3.41 and 2.90 in the GFNP (95% CI: -3.05 to 9.86) and in the GRNP (95% CI: -2.65 to 8.46) respectively (Figure 5.3c). Group size was a strong predictor of change in alarm calls (AIC weight = 1), with change in alarm calls increasing by 0.54 calls with every additional individual present (95% CI: 0.13 to 0.95). All other variables were not strongly supported predictors

of change in alarm calls per minute: distance to settlements (parameter estimate: -16.30; 95% CI: -20.38 to 12.23, AIC weight = 0.25), tree height (parameter estimate: 0.22; 95% CI: -0.20 to 0.26, AIC weight = 0.14) and reaction distance (parameter estimate: 0.08; 95% CI: -0.07 to 0.10, AIC weight = 0.17).

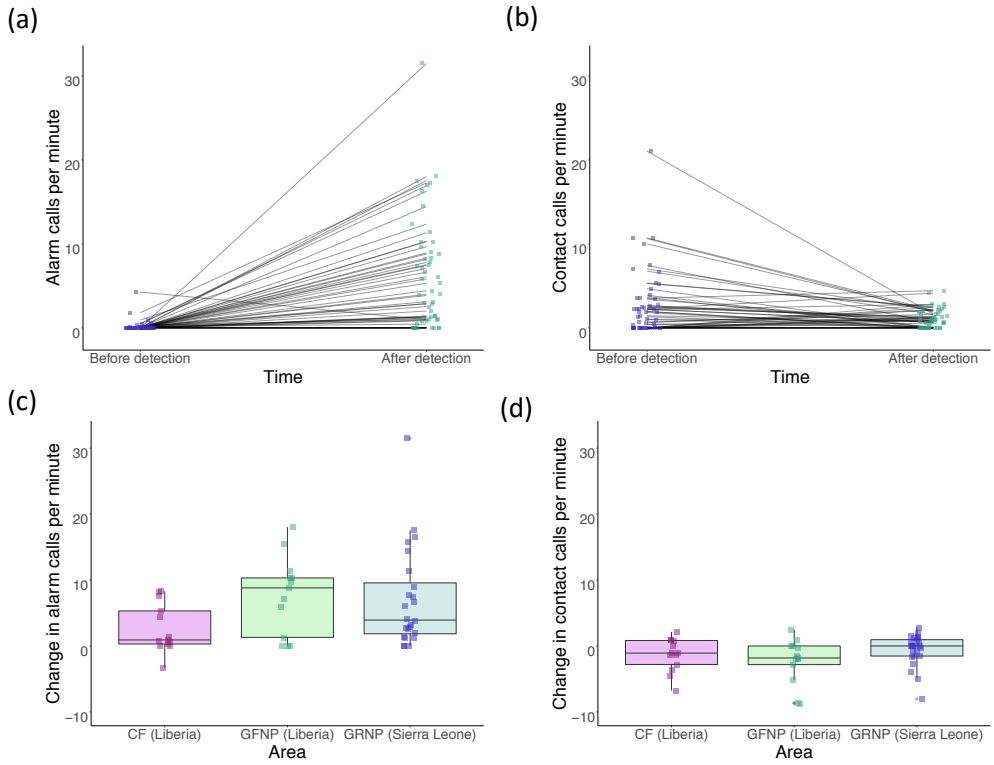

Figure 5.3 Overall changes in number of alarm calls (a) and contact calls (b) per minute produced before and after detection. Differences in alarm vocalisation change (c) and contact vocalisation change (d) between law enforcement areas. Box plots show first quartile, median and third quartile, vertical lines show ranges excluding outliers, dots show the raw data

Change in contact calls was best explained by five predictors (Table 5.2), though none of the variables were strongly supported predictors of change in contact calls per minute: group size (parameter estimate: -0.88; 95% CI: -2.89 to 1.12, AIC weight = 0.59), tree height (parameter estimate: -0.04; 95% CI: -0.22 to 0.13, AIC weight = 0.32), undergrowth (parameter estimate: -0.00; 95% CI: -0.03 to 0.03, AIC weight = 0.09) and reaction distance (parameter

estimate: 0.03; 95% CI: -0.04 to 0.09, AIC weight = 0.48). Law enforcement area was also not a strong predictor of change in contact calls per minute (AIC weight = 0.37): change in contact calls was intermediate in the community forest (mean = -9.14; 95% CI: -26.73 to 8.46), decreased by 0.22 in the GFNP (95% CI: -1.57 to 1.14) and increased by 0.29 in the GRNP (95% CI: -1.07 to 1.65) (Figure 5.3c). The null model (AIC weight = 0.09) was present in the top models (Table 5.2), suggesting none of the hunting variables are good predictors of change in contact calls in Diana monkeys.

Table 5.2 Top candidate models exploring change in Diana monkey reaction behaviour

Response	model	k	AICc	ΔAICc	weight
FID	height + area	5	438.56	0.00	0.41
	height + n.species + area	6	439.74	1.19	0.23
	height + undergrowth + area	6	439.86	1.31	0.21
	height + n.species + undergrowth + area	7	440.54	1.99	0.15
Fleeing time	group size + area	5	300.07	0.00	0.53
	fruit + group size + area	6	301.45	1.39	0.26
	group size + n.species + area	6	301.94	1.87	0.21
Change in visibility	area	4	113.98	0.00	0.45
	null	2	114.30	0.32	0.38
	signs	3	115.89	1.91	0.17
Inspection	group size + undergrowth + distance	4	78.92	0.00	0.36
	group size + height + undergrowth + distance	5	79.38	0.46	0.29
	group size + height + distance	4	80.31	1.39	0.18
	group size + height + undergrowth	4	80.53	1.61	0.16
Change in alarm calls	group size + area	5	328.22	0.00	0.31
	group size + distance	4	328.66	0.43	0.25
	group size + reaction distance + area	6	329.43	1.21	0.17
	group size + height + area	6	329.80	1.58	0.14
	group size	3	330.00	1.78	0.13
Change in contact calls	group size	3	245.83	0.00	0.11
	null	2	246.28	0.45	0.09
	group size + height + reaction distance	5	246.34	0.51	0.09
	group size + reaction distance	4	246.53	0.70	0.08
	reaction distance	3	246.54	0.71	0.08
	group size + area	5	246.73	0.89	0.07
	group size + height	4	246.77	0.94	0.07
	group size + reaction distance + area	6	246.96	1.12	0.06
	height + reaction distance	4	247.01	1.18	0.06
	group size + height + reaction distance + area	7	247.24	1.40	0.06
	reaction distance + area	5	247.28	1.45	0.05
	group size +undergrowth	4	247.43	1.59	0.05
	area	4	247.65	1.81	0.04
	height	3	247.73	1.90	0.04
	undergrowth	3	247.74	1.91	0.04

***** area = law enforcement area, distance = distance to settlements, signs = encounter rate of hunting signs, height = mean tree height, undergrowth = undergrowth visibility, fruit = presence of fruit, group size = number of monkeys in a group, n.species = number of species present, reaction distance = distance at which monkeys detect the observer, null = null model

Table 5.3 Top candidate models exploring change in lesser spot-nosed monkey reaction behaviour

Response	model	k	AICc	ΔAICc	weight
FID	group size + height + n.species + area	7	180.52	0.00	0.28
	group size + n.species + area	6	180.55	0.03	0.28
	fruit + group size + n.species + area	7	181.01	0.49	0.22
	height + n.species + area	6	182.16	1.65	0.12
	group size + distance	4	182.48	1.96	0.10
Fleeing time	n.species	3	102.97	0.00	0.50
	group size + n.species	4	102.99	0.03	0.50
Change in visibility	n.species + area	5	77.68	0.00	1.00
Inspection	signs	2	26.25	0.00	0.47
	n.species + signs	3	26.89	0.64	0.34
	n. species	2	27.97	1.72	0.20

***** area = law enforcement area, distance = distance to settlements, signs = encounter rate of hunting signs, height = mean tree height, fruit = presence of fruit, group size = number of monkeys in a group, n.species = number of species present

5.4 Discussion

This chapter explored what effect variation in human hunting pressure may have on reaction antipredator defences of Diana monkeys and lesser spot-nosed monkeys. Both species were expected to exhibit stronger avoidance behaviours where the pressure from human hunting was higher, with Diana monkeys showing stronger responses given the higher vulnerability to hunting of this species compared to lesser spot-nosed monkeys. Overall, both species showed changes in behavioural reaction to human presence linked to degree of hunting pressure, suggesting a plastic behavioural response to human hunting pressure in Gola.

Both species had a longer FID in the community forest of Liberia compared to the GRNP in Sierra Leone. This supports the hypothesis that monkeys adapt reaction defences to variation in human predation, fleeing at larger distances in areas experiencing higher levels of hunting pressure. This is consistent with studies on birds and ungulates that found longer FIDs in areas with higher human hunting (de Boer et al. 2004; Setsaas et al. 2007; Magige et al. 2009; Tarakini et al. 2014). No previous study has looked directly at FID linked to hunting pressure in primates. A study by Mikula et al. (2018) measured FID in vervet monkeys, *Chlorocebus pygerythrus*, in urban and rural environments and found shorter FIDs in urban environments, presumably caused by higher habituation in cities but likely also by a higher perception of risk in rural areas (as monkeys are sometimes killed by farmers as pests or hunted for wildmeat).

Diana monkeys fled faster in the community forest (CF) of Liberia compared to the GRNP of Sierra Leone. This result further supports changes in avoidance reaction defences with level of hunting, with monkeys fleeing faster in areas with higher hunting pressure. Furthermore, larger groups of Diana monkeys took longer to flee compared to smaller ones, likely because it takes less time for fewer monkeys to flee. This could also suggest lower risk perception in larger groups, supporting the risk 'dilution effect' hypothesis (Lima 1990). Similarly, lesser spot-nosed monkey fled slower when more species were present. No association however was found between hunting pressure and fleeing time in lesser spot-nosed monkeys.

Law enforcement area was a strong predictor of change in visibility in lesser spot-nosed monkeys. The species became less visible following detection in both the community forest and the GFNP in Liberia and became more visible in the GRNP in Sierra Leone. Contrary to expectations, there was no difference in Diana monkey change in visibility with level of hunting pressure, with Diana monkeys generally becoming more visible following detection across the whole study site. Papworth et al. (2013) also found no difference in change in visibility with hunting pressure in woolly monkeys, *Lagothrix poeppigii*, however in their study the change was always negative rather than positive. Results in this study contrast with findings in Taï National Park, Ivory Coast, where Diana monkeys were found to hide consistently in the presence of humans in hunted areas compared to unhunted

ones, where in contrast the monkeys were very exposed (Koné and Refisch 2007).

The increase in visibility of Diana monkeys could be linked to their high probability of inspection across the study region, independent of hunting pressure. This result is in line with findings in Taï National Park where Diana monkeys showed strong inspection behaviour in the presence of humans in both a hunted and an unhunted area (Koné and Refisch 2007). This species typically inspects predators before fleeing in contrast with lesser spot-nosed monkeys which show a considerably lower probability of inspection, with no variation linked to hunting pressure. Inspecting behaviour is very risky, as animals inevitably become more vulnerable to attack (Lima and Dill 1990), thus it is not surprising that probability of inspection decreased in smaller groups.

A number of studies have observed a reduction in vocalisation levels in primates as a reaction to human presence in areas experiencing high hunting pressure (Zuberbühler et al. 1997; Bshary 2001; Kümpel et al. 2008; Dooley and Judge 2015). Results from this study, however, find no conclusive evidence of hunting pressure changing vocalisation following detection in Diana monkeys. Diana monkeys sounded significantly more alarm calls after detection throughout the study region. This result is in accordance with Croes et al. (2006) that find monkey groups sounded alarm calls around 70% of the time after detecting observers in both a hunted and an unhunted site. The

study only recorded presence or absence of alarm calls however, and not the frequency of those calls.

Findings in this study contrast results in Bshary (2001), where a reduction in total number of Diana monkey calls was recorded in response to playbacks of predator or prey imitation calls by humans in a hunted area. Furthermore, Zuberbühler et al. (1997) found Diana monkeys became silent in response to approaching humans and Kümpel et al. (2008) found that black colobus, *Colobus satanas*, stopped calling around the village when in contact with humans. This reduction in vocalisation reflects the expected reaction against pursuit hunters such as humans and chimpanzees. A similar reduction in vocalisation, in fact, is seen in red colobus, *Piliocolobus badius*, as a reaction to chimpanzee calls (Boesch 1994). It is surprising that in this study Diana monkeys increase their alarm calls as a reaction to human presence throughout the study region. Although contact calls were significantly reduced following detection, the overall call rate was higher, clearly making the groups more conspicuous to pursuit predators such as humans. It could be that, since monkeys had already been detected by the observers, calling did not enhance detectability as they were already detected. Furthermore, overall number of calls per minute were significantly lower in this study compared to unhunted regions in other studies (Bshary 2001), suggesting that despite an increase in call rate following detection, frequency of calls was still low compared to areas with no human hunting pressure.

Overall, results suggest that both species adjust some response defences to human presence to changes in hunting intensity, with both species having larger FIDs, Diana monkeys fleeing faster and lesser spot-nosed monkeys becoming less visible in area which experienced more hunting. Law enforcement area was the strongest hunting predictor, suggesting monkeys are adapting their behaviour over longer time periods than can be captured with 'snapshot' methods that measure the current state of hunting pressure (such as encounter rate of hunting signs and frequency of gunshots). As highlighted in Chapter 4 (*4.4 Discussion*), no area of the study region is truly unhunted, and thus it becomes difficult to record any marked potential differences in behaviour. Conducting a similar study with a true unhunted "control" area would be an interesting avenue for further work.

Contrary to expectations, no strong difference in response was observed between species, with both species increasing avoidance behaviours in response to hunting. Descriptive statistics for Campbell's monkeys, *Cercopithecus campbelli*, and sooty mangabeys, *Cercocebus atys*, however, suggest no changes in response defences of these two species to hunting, apart from FID in Campbell's monkeys (Appendix 3). This pattern would perhaps change with a larger sample size but also highlights potential variation amongst species that should carefully be considered. Despite lesser spot-nosed monkeys reportedly being less vulnerable to hunting by humans (Oates 2011), a bushmeat market survey in eastern Libera found lesser spot-nosed monkeys (25%) and Diana monkeys (19.3%) were the most abundance primates present, suggesting a strong predation pressure from humans on this

species (Covey and Mcgraw 2014). It is therefore not surprising that lesser spot-nosed monkeys are also adapting their behaviour in response to human predation pressure.

Recorded behavioural changes in this study reflect hunter reports in a study in Central African Republic, where 88% of hunters thought that primates had changed their behaviour in response to the increase in gun hunting, becoming harder to detect (Robinson et al. 2011). These adaptations, in fact, likely have a strong impact on detection probabilities for both hunters and researchers and thus may have potential implications for density estimates of the species. The next chapter will explore the potential effects that some of these reaction defences may have on our estimations of primate populations.

Chapter 6

Avoidance behaviours in density estimates of primate populations: an agent-based modelling approach

6.1 Introduction

Over the past few decades, unsustainable hunting, primarily driven by an increase in demand and a shift towards commercial practices, has had vast detrimental effects on species numbers in many tropical forest ecosystems (Milner-Gulland et al. 2003; Wilkie et al. 2011; Benítez-López et al. 2017). The most affected by the rise in hunting pressure are large mammals, including ungulates and primates (Robinson and Bennet 1990; Ripple et al. 2016). To measure population change through time and space, evaluate hunting sustainability and assess the effectiveness of conservation interventions, it is becoming increasingly important to effectively monitor population numbers of hunted species (Bawa and Menon 1997; Rist et al. 2009; da Silva Chaves et al. 2019). Surveying species under hunting pressure however, can be challenging, as they often occur at low densities and have likely adapted their behaviour to minimise detection by human 'predators' (Fa and Brown 2009). As seen in the previous chapters, there is various

evidence that describes changes in behaviour in species as a result of hunting. Kiffner et al. (2014) found that some ungulate species significantly altered their response to human presence according to the level of law enforcement. Similarly, the flight initiation distance (FID) of impala and greater kudu was shorter in a protected area in Zimbabwe compared to hunted areas outside the park (Tarakini et al. 2014).

In Central and West Africa, primates are one of the orders under highest threat by hunting: constituting an estimated 20% of the trade in wild meat markets (Fa and Brown 2009), comprising 19% of all recalled harvested carcasses by hunters in the Gola forest of Liberia (Jones et al. 2019) and constituting between 25% and 39% of the total biomass of wild meat found in restaurants around Taï National Park in Côte d'Ivoire (Refisch and Koné 2005). Avoidance behavioural responses analogous to those found in ungulates have been recorded in primates. Black colobus monkeys, *Colobus satanas*, were found to immobilize more often (Kümpel et al. 2008) and Diana monkeys, *Cercopithecus diana*, reduced their vocalization levels (Bshary 2001) in areas subject to higher hunting intensity. Evidence of avoidance behaviours in primates was also found in this study. As seen in Chapter 5, Diana monkeys and lesser spot-nosed monkeys increased their flight initiation distance and reduced their fleeing time in areas under greater hunting intensity. A combination of lower densities and increased avoidance behaviours in hunted regions is therefore likely to impact the probability of detecting a species during monitoring to estimate population densities. Some evidence of the effect of behavioural change on density estimates is available from research

in marine ecosystems. Robertson et al. (2016) found that altered diving behaviour in bowhead whales, induced by seismic operations, resulted in underestimations of species numbers from aerial surveys. Behavioural change is also likely to impact detection probabilities of terrestrial mammals, potentially affecting density estimates of hunted species. But how can we assess whether an increase in avoidance behaviours affects density estimates?

Distance sampling (Buckland et al. 2001) is probably the most widely used method currently adopted to estimate population densities, particularly for mammals (Endo et al. 2010) and birds (Marsden 1999; Magige et al. 2009; Suwanrat et al. 2015). Unlike more traditional survey techniques such as plot sampling, this method accounts for uncertain detection scenarios where not all study objects within the survey area are detected (Miller et al. 2013). Distance sampling incorporates detection probability in modelled predictions of density by using distance from the line/point to the study object (individual/group/sign) to fit a detection function, with probability of detection usually decreasing with increasing distance (Thomas et al. 2010). Two of the key distance sampling assumptions are 1.that all individuals on the line or point are detected, and 2. that individuals do not move in response to observers prior to being detected (Thomas et al. 2010). As highlighted in Chapter 1 (*1.4 Detectability and density estimates*) however, these assumptions may not always be met, especially under conditions where human presence is perceived as a threat, such as under high levels of hunting pressure (Table 1.1). If animals freeze more often for example, this may result in animals being less conspicuous, especially within high canopy forests.

This in turn may bias the assumption of certain detection on the line, leading to density estimates which are biased low (Buckland et al. 2001).

Furthermore, distance sampling primarily models detectability as a function of distance, although covariates of detection probability (i.e. behaviour) can be included in multiple covariate distance sampling (MCDS) (Buckland et al. 2001). It can be difficult, however, to collect behavioural data alongside distance sampling data, given the different methods of data collection. Moreover, even when adding covariates to the model, the main distance sampling assumptions remain. Density estimates resulting from modelling covariates with a statistical approach therefore are still linked to assumptions associated with modelling of the detection function.

Agent-based (also known as individual-based) models offer a bottom-up approach in which outputs emerge from interactions amongst 'agents' who behave according to a set of assigned rules (Railsback and Grimm 2019). One advantage is that each individual can be assigned any number of rules and thus these models can be useful when high individual variation is present. Agent-based models can also be useful when modelling individual interactions as well as adaptive behaviours and ultimately aim to study how system level properties come about (DeAngelis and Grimm 2014). Agent-based models are increasingly being applied to model social and biological systems (DeAngelis and Grimm 2014). They have been used, for example, to predict antipredator behaviour of schooling fish (Vabø and Nøttestad 1997), to model tiger population dynamics (Carter et al. 2015), to estimate collision

risks of predatory birds with wind turbines (Eichhorn et al. 2012), to understand interactions between social and ecological systems (Iwamura et al. 2014) and to simulate spread of knowledge of ranger patrol presence amongst hunting communities (Dobson et al. 2019a). To the best of our knowledge, agent-based modelling has never been implemented to predict the effects of behavioural covariates on a species' density estimate.

This study aims to understand what effect behavioural change linked to human hunting pressure may have on density estimates of primate populations. This question is addressed by implementing an agent-based modelling approach which allows simulation of the detection process given a set of behavioural rules derived from empirical data under different hunting scenarios. Specifically, the study focusses on West African forest dwelling monkeys, given their high vulnerability to hunting, and the model is parameterised using monkey behavioural data recorded during this study (Chapter 5). This model simulates the behaviour of an observer walking line transects in a tropical forest to estimate the density of monkey groups. The distance at which monkey groups will flee from the approaching observer (FID) and the ability of the monkey groups to detect the observer will vary depending on hunting intensity. Since, as shown in Chapter 5 (*5.3 Results*), law enforcement area was a strong predictor of behavioural change, a "high hunting" and a "low hunting" scenario were compared based on degree of law enforcement. I hypothesise that avoidance behaviours linked to hunting are likely to reduce detection on the transect line and/or cause detection of monkeys away from their initial locations (Table 1.1), ultimately negatively

impacting density estimates in areas under increased hunting pressure. More specifically, longer FIDs and a greater detection ability by monkeys in areas with greater hunting pressure may result in monkeys responding to observer presence prior to detection by the observer. If monkeys flee beyond the observer's detection range, this will likely lead to density estimates that are biased low in those areas (Buckland et al. 2001).

6.2 Methods

6.2.1 Study system

The model simulation is based on empirical data collected in the Gola region of Liberia and Sierra Leone in West Africa. As seen in Chapter 2 (*2.1.1 Location*), the region is subject to varying levels of hunting pressure across different management areas. Behavioural data on two West African monkey species was collected between October 2017 and May 2018 along transect lines (2-4km) across the Gola region. Diana monkeys, *Cercopithecus diana*, and lesser spot-nosed monkeys, *Cercopithecus petaurista*, were chosen given their high exposure and vulnerability to hunting pressure in West Africa (McGraw et al. 2007; Covey and Mcgraw 2014) and because they can be found across the Gola area (pilot survey May-June 2017). Furthermore, as these species were encountered more often compared to others, larger sample sizes allowed for better informed model parameterisation. For further information on behavioural data collection and analysis see Chapter 2 (*2.3*

Data collection, 2.4 Data processing and analysis), Chapter 4 (*4.2 Methods*) and Chapter 5 (*5.2 Methods*).

Behavioural variables used for model parameterisation include the distance at which monkey groups flee from the approaching observer (flight initiation distance – FID). This parameter was chosen given the significant differences observed between the different hunting pressure areas in Gola (see Chapter 5, *5.3.1 Flight initiation distance (FID)*). Furthermore, the ability of the monkey groups to detect the observer was parameterised from recorded reaction distances. In the model simulation two hunting scenarios were compared: 1) A "low hunting" scenario, parameterised with data collected in the Gola Rainforest National Park (GRNP) in Sierra Leone, a protected area with established on the ground law enforcement in the form of regular patrolling; 2) A "high hunting" scenario, parameterised with data collected across the border in Liberia, where the community forest had no enforced hunting regulations at the time of data collection (2017-2018).

6.2.2 Model Description

The description of the agent-based model follows the ODD (Overview, Design concepts, Details) protocol devised by Grimm et al. (2006) and updated by Grimm et al. (2010). This description comprises seven sections: the first three give an overview of the model, the fourth expands on the general concepts that underly the model design and the last three give in depth details of the model (Grimm et al. 2006).

6.2.2.1 Purpose (Section 1)

The overarching purpose of the model is to understand and measure the effect that avoidance behaviours may have on density estimates, in order to draw attention to potential biases in census results linked to variation in hunting pressure. An understanding of these potential biases may encourage the development of an agent-based modelling approach to explore the indirect effect of avoidance behaviours on other species' density estimates. Quantifying the possible bias may ultimately inform more accurate sustainability predictions and a better categorisation of species under international conventions. Specifically, this model aims to explore whether changes in FID, and shifts in probability of detecting humans linked to hunting, affect density estimates of Diana monkeys and lesser spot-nosed monkeys in a tropical forest habitat.

6.2.2.2 Entities, state variables, and scales (Section 2)

Entities can be described as the agents in the model, their state variables are the characteristics that define those entities and distinguish them from others and scales refers to the temporal and spatial scales of the model (Grimm et al. 2006). This model simulation has two types of entities: an observer (i.e. researcher) entity and the monkey groups (Figure 6.1, Table 6.1). Observer state variables are grid location and the detection function that defines the observer's probability of detecting a monkey group at a particular distance. Monkey group state variables are initial location, species and reaction

behaviour. Monkey group reaction behaviour depends on the intensity of hunting pressure and includes the monkey group detection function (defined as the probability of monkeys detecting the observer) and the FIDs at which monkey groups run away at the approach of the observer (Table 6.1).

A collective of entities can also possess its own state variables. Here, the aggregate entity is the total number of monkey groups (i.e. group density) (Table 6.1). Monkey groups, as opposed to individuals, are modelled, since it is often the density of groups that is calculated in primate distance sampling, given the difficulty in accurately calculating group size in a forest environment (Brugiere and Fleury 2000).

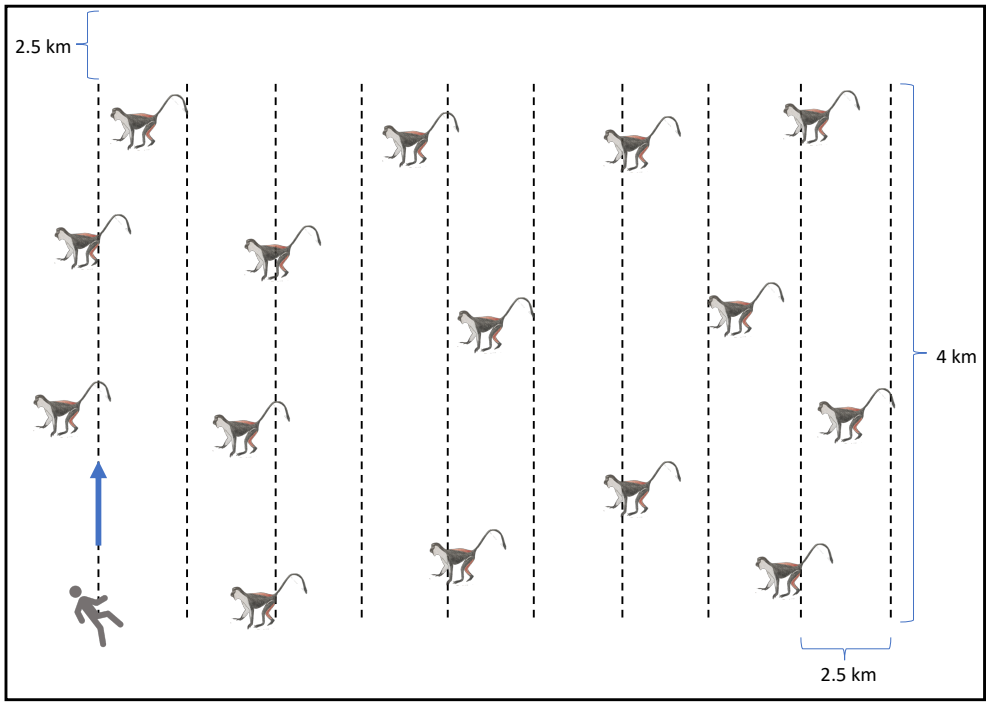

Figure 6.1 Schematic representation of the spatial landscape of the model showing the distribution, length and spacing of transect lines, the observer starting location and the uniformly distributed monkey groups. Each monkey represents a monkey group. The true model landscape is comprised of 60 parallel transect lines

The spatial scale of the model is a two-dimensional 147.5 km by 9 km grid (1327.5 km^2), with a total of 60 transect lines of length 4 km placed 2.5 km

apart with a 2.5 km buffer around the edge (Figure 6.1). This landscape design was chosen as it reflects transect length and spacing in the Gola Forest. The number of transects was chosen so that a minimum of 60-80 detections (minimum suggested sample size for reliable fitting of the detection function - (Buckland et al. 2001)) could be made at each iteration. Each transect line is walked by the observer entity in 80-time steps, with each time step corresponding to 50 metres (3 minutes), for a total of 240 km of survey effort (corresponding to 240 hours) for each iteration.

Time step length of 50 metres was chosen as this is the spacing suggested for marking transect lines during distance sampling (Peres 1999). The conversion to time units is based on average observer speed during distance sampling, which is usually around 1 km/h (Peres 1999). The model did not permit entities to move outside spatial boundaries.

6.2.2.3 Process overview and scheduling (Section 3)

Here, the environmental and individual processes built in the model are described as well as how these processes are scheduled and ordered (Grimm et al. 2006). The processes involved in the model comprise movement and encounter events. These include the *movement of the observer* along transect lines, the *baseline movement of monkey groups*, *monkey group fleeing,* as well as the *detection of the observer by the monkey groups* and the *detection of the monkey groups by the observer*.

Table 6.1 Parameter table and variable sources selected for model simulation

Entities	Parameters	Low hunting	High hunting	Definition	Source
Region	Grid size X Y (metres)	147500 x 9000	147500 x 9000	Size of the study region	-
	Transects	60	60	Number of transect lines	-
	Length (m)	4000	4000	Length of transect lines	-
Observer	Observer speed - steps per transect (step length - m)	80 (50)	80 (50)	Density survey speed	Peres (1999)
	Observer detection model (hazard rate)	Shape = 2 Scale = 27	Shape = 2 Scale = 27	Probability of detection curve shape and scale parameters	This study
Monkey groups	Position of monkey groups	Uniform distribution	Uniform distribution	Monkey group location across the landscape	-
	Density of monkey groups per km^2	4	2.5	Total number of monkey groups present in study region	Realistic densities based around Klop et al. 2008 and more recent (2016) GRNP density survey
	Monkey detection model (hazard rate)	Scale = 25 Shape = 2	Diana: Scale = 38 Diana: Shape = 3 Spot-nosed: Scale = 41 Spot-nosed: Shape = 3	Probability of detection curve shape and scale parameters	This study
	Flight initiation distance (m)	Sample from empirical FIDs for low hunting location	Sample from empirical FIDs for high hunting location	Distance at which monkey groups move from observer	This study
	Baseline speed	Sampled from an exponential distribution, k=0.15	Sampled from an exponential distribution, k=0.15	Baseline movement of monkey groups at each time step	Parameterised from average daily group travel distances (Oates 2011)
	Fleeing speed	Sampled from a normal distribution, mean =60, SD=10	Sampled from a normal distribution mean=60, SD=10	Fleeing speed of monkey groups after detecting the observer	Parameterised from observed Cercopithecus monkey fleeing distances (Croes et al. 2006)

The model proceeds in discrete time steps, at each time step the observer moves along a transect line. If, at a time step, the probability function of the observer causes a monkey group to be detected, the perpendicular distance between the group and the transect line will be calculated and stored. To avoid double counting a group, the model will remove all groups already detected by the observer. If, at a time step, a monkey group (given its detection probability function) detects the observer and is located at a distance shorter or equal to its FID, at the following time step those monkey groups will move in the opposite direction to the observer. If the observer is not detected, baseline movement of monkey groups follows a random pattern. The only state variable that changes at each time step is the location of the entities (both observer and monkey groups). The observer movement continues along transect lines irrespective of encounter events, the monkey group movement follows random movement patterns and can change direction and increase in speed if the observer is detected. Other entity state variables change only between scenarios.

6.2.2.4 Design concepts (Section 4)

This section provides details on the broader concepts that underpin the model's design.

Basic principles: The movement of the observer along transect lines and the calculation of perpendicular distances are related to classic distance sampling methodology. The detection function and the FIDs of the monkey groups are

based on species-specific data. In order to be re-used and adapted to other species the model would have to be parameterised using context specific empirical data.

Emergence: Number of detected groups and perpendicular distances between detected monkey groups and the transect line emerge from the reaction behaviours of the monkey groups.

Objectives: The monkey group's objective is to avoid detection by the observer. The observer objective is to detect monkey groups.

Sensing: Monkey groups are assumed to know whether they are in a high hunting or a low hunting area so they can apply area specific behavioural rules to respond to the presence of the observer.

Interaction: Direct interactions occur between monkey groups and the observer, as the observer walks along transect lines, simulating the data collection process.

Stochasticity: The initial distribution of monkey groups is determined stochastically from a uniform distribution. Monkey group baseline speed at each time step is taken from a random exponential distribution and monkey group fleeing speed is taken from a normal distribution. Both these distributions are empirically determined. Monkey group baseline direction of

movement at each time step is also determined stochastically. Detections are determined by probability distributions parameterised from field data.

Observation: The outputs observed to test model predictions are the number of monkey groups detected by the observer, the perpendicular distances between detected monkey groups and the transect lines, sampling effort and total area. All outputs are saved to spreadsheets after each iteration and are used in model analysis to fit the detection function and calculate a density estimate.

6.2.2.5 Initialization (Section 5)

Here the initial state of the model at time step one is described. The model is always initialised with the observer entity at the start of the first transect (Figure 6.1). The model explores how the number of detections and the distribution of perpendicular distances vary as a consequence of the initial state of the monkey group entities. The monkey group entities vary in number, assigned detection function and FIDs between the high hunting and the low hunting simulations (Table 6.1).

6.2.2.6 Input data (Section 6)

This section describes the dynamicity of state variables (i.e. how these may change during the running of the model). The model does not use input data to represent time-varying processes.

6.2.2.7 Submodels (Section 7)

This section elaborates and explains in more detail the processes listed in "Process overview and scheduling". All model parameters are listed in Table 6.1.

The *movement of the observer* is a fixed speed along transect lines and reflects distance sampling field methodology. When the observer reaches the end of a transect, they start the next transect at the following time step.

The *baseline movement of monkey groups* at each time step can follow any direction, sampled from a uniform distribution, and the monkey speed is taken from a random exponential distribution with a rate parameter of 0.15 (Figure 6.2a). This distribution was chosen since the resulting curve has a long-tailed distribution, with animals mostly moving short distances around the group's initial location and occasionally moving longer distances (i.e. traveling). This behaviour resembles monkey group movements around a home range (Oates 2011). Since both Diana monkeys and lesser spot-nosed monkeys have an average daily group travel distance of around 1km (Oates 2011), and the average day length in West Africa is around 12h, the mean baseline distance travelled by a monkey group per time step was calculated as follows:

$$\left(\frac{mean\ distance\ travelled\ per\ day(metres)}{day\ length\ (minutes)}\right) \times time\ step\ length\ (minutes)$$

$$= \left(\frac{1000}{720}\right) \times 3 = 4.2\ m/t$$

The rate parameter of the exponential distribution was then chosen so that the mean distance travelled by monkey groups per time steps falls in the most frequent bin (Figure 6.2a).

Monkey group fleeing is determined by the position of the observer at the previous timestep. If the monkey group detects the observer and the distance between the observer and the monkey group is less than the FID (sampled from a vector of recorded distances from either the high hunting or the low hunting region), the monkey group direction of movement follows a Von-Mises distribution with direction (mu) opposite to the observer and a concentration parameter kappa = 50 (Figure 6.2c). Monkey group fleeing distance was sampled from a normal distribution with a mean of 60 and a standard deviation of 10 (Figure 6.2b). Fleeing distance was parameterised from observed Cercopithecus monkey fleeing distances (Croes et al. 2006).

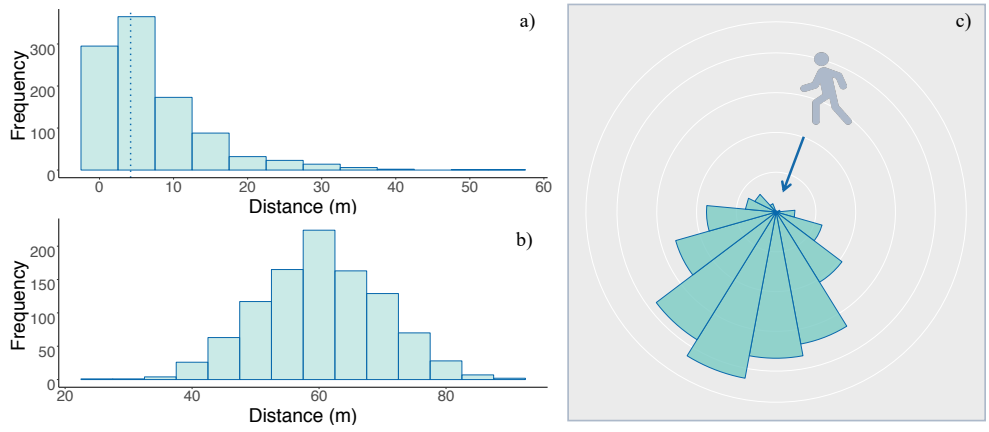

Figure 6.2 Monkey group baseline distance moved at each time step sampled from an exponential distribution with a rate parameter of 0.15 (a), monkey group fleeing distance sampled from a normal distribution with mean 60 and a standard deviation of 10 (b). Von-Mises distribution (kappa = 50) illustrating the fleeing direction of monkey groups relative to the observer position (c)

The monkey group detection function follows classic distance sampling hazard-rate curves (Hayes and Buckland 2006) and is used as a proxy for overall vigilance efficiency under different hunting scenario. A hazard-rate model was chosen as it has an underlying model developed for the detection process (Hayes and Buckland 1983, Buckland et al. 2010). Furthermore, it allows for higher levels of flexibility, as both a scale and a shape parameter can be set. Two detection functions for each species were parameterised from reaction distances recorded in areas with low and high hunting respectively, during fieldwork data collection (detailed in Chapter 2, *2.3 Data collection*). The reaction distance is defined as the distance at which animals detect the observer. To model detection probability, median reaction distances recorded in the field are assumed to coincide with the detection probability falling to 0.5 (Figure 6.3). In the resulting models, for the low hunting area detection is certain up to around 15 metres and declines to 0.5 at 30 metres for both species (Equation 1); for the high hunting area detection is certain up to around 25 metres and declines to 0.5 at 43 metres for Diana monkeys (Equation 2) and at 46 metres for lesser spot-nosed monkeys (Equation 3):

Detection function of both species in low hunting area (scale=25, shape=2)

1) $g(y) = 1 - exp\{1 - (y/25)^{-2}\}$

Detection function of Diana monkeys in high hunting area (scale=38, shape=3)

2) $g(y) = 1 - exp\{1 - (y/38)^{-3}\}$

Detection function of lesser spot-nosed monkeys in high hunting area (scale=41, shape=3)

3) $g(y) = 1 - exp\{1 - (y/41)^{-3}\}$

where g(y) is the probability that the observer is detected at distance *y*.

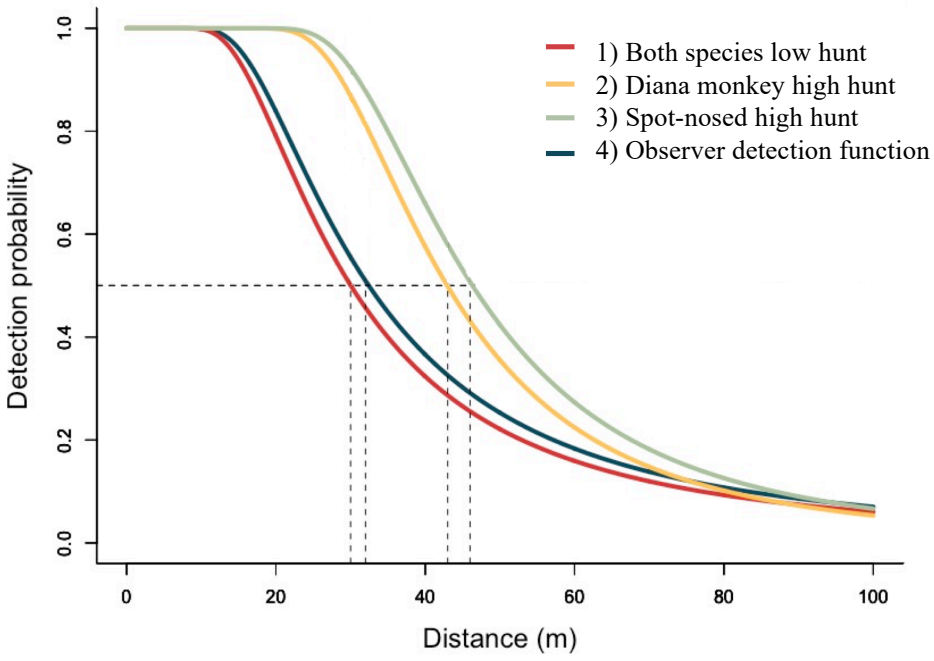

Figure 6.3. Detection functions parameterised from field data for the model simulation. A detection probability of 0.5 coincides with the median recorded reaction distances for each species under different levels of hunting intensity

The observer detection function also follows classic distance sampling detection curves (Equation 4). The detection function is parameterised from the distances at which monkey groups were detected during field data collection. The median detection distances recorded in the field are assumed to coincide with the detection probability falling to 0.5. Here, detection is certain up to 15 metres and declines to 0.5 at around 32 metres (Figure 6.3):

Detection function of the observer (scale=27, shape=2)

4) $g(y) = 1 - exp\{1 - (y/27)^{-2}\}$

To define detection events (i.e. detected or not detected) from detection probability functions, Bernoulli trials were used, with probability given by the appropriate detection functions at the given distance.

6.2.3 Simulation experiments

Different simulation scenarios were run to test the potential indirect effect that variation in hunting pressure may have on distance sampling assumptions and consequently on density estimates, with 100 iterations for each scenario. All combinations of the different behavioural parameters were modelled under different scenarios to identify any discernible patterns (Table 6.2).

A sensitivity analysis was carried out in order to assess whether observer step length and monkey group mean fleeing speeds might have an effect on model outputs. Scenarios A and D were run for Diana monkeys with a starting density of 2.5 groups/km^2. Upper and lower parameter limits for both step length and mean fleeing speeds were selected by halving and doubling the baseline values. I considered this substantial variation to detect any major effects on final density estimates.

Table 6.2 The different model simulation scenarios. All combinations were run for both Diana monkeys and lesser spot-nosed monkeys at different starting densities. Low refers to "low hunting" data and high refers to "high hunting" data

Scenario	Density 2.5 groups/km^2	Density 4 groups/km^2
A	Low FID and low detection	Low FID and low detection
B	Low FID and high detection	Low FID and high detection
C	High FID and low detection	High FID and low detection
D	High FID and high detection	High FID and high detection

6.2.4 Model analysis

The model was build and all analysis was conducted in R Studio v.1.1.456 (R Core Team 2018). Resulting perpendicular distances were then analysed using the "*Distance"* package (Miller et al. 2016) in R Studio to generate density estimates that were then compared to the actual densities used as the model inputs under different scenarios. To improve robustness of distance sampling analysis, a truncation distance of 100 m was selected. All graphs were produced in "*ggplot2*" (Wickham 2016).

6.3 Results

Overall, all scenarios resulted in fairly accurate density estimates that closely reflected actual densities used as model inputs. Furthermore, no major differences were found between the different scenarios (Figure 6.4). However, under the scenario with high FID and high detection (i.e. "high hunting"- Scenario D) the 95% confidence interval did not overlap with the actual density and in all cases lay below it (Figure 6.4). In contrast, under the

scenario with low FID and low detection (i.e. “low hunting”- Scenario A) the 95% confidence interval always includes the actual density (Figure 6.4). However, when looking at the accuracy of each iteration, there is no difference between scenarios in the percent of cases in which the 95% confidence interval of the estimated density includes the actual density (Figure 6.5).

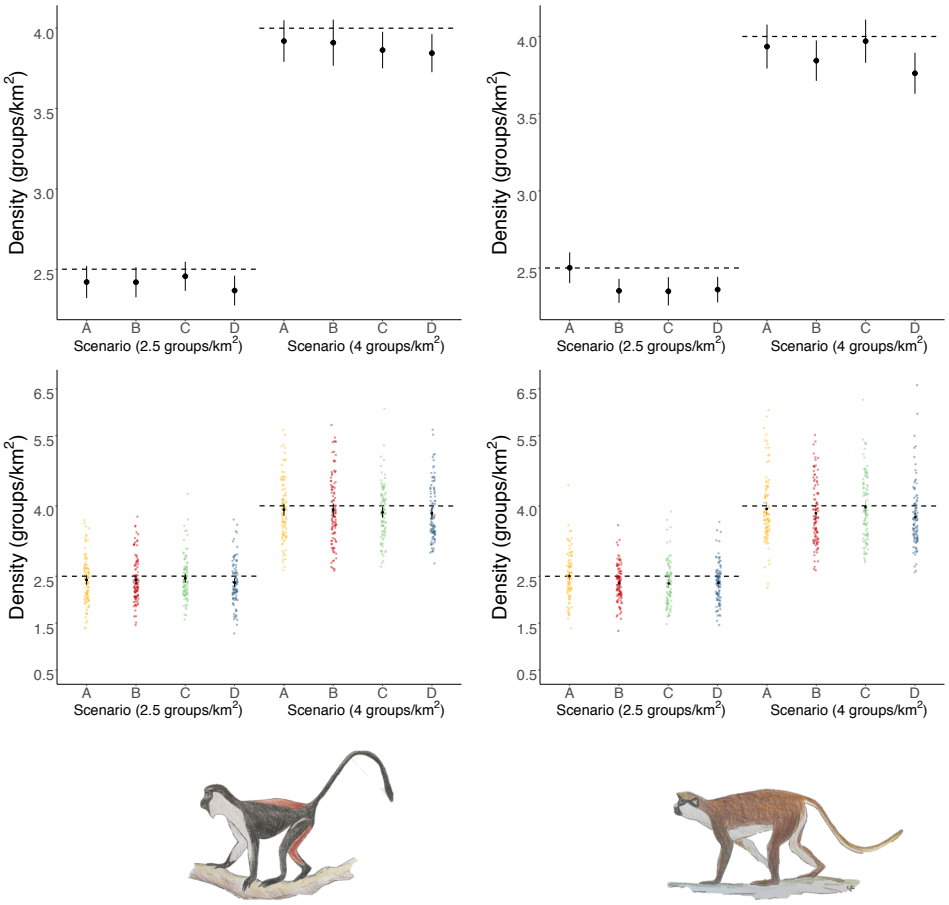

Figure 6.4 Top graphs show the mean density estimates and their 95% confidence intervals across the 100 iterations under each scenario. Bottom graphs show the spread of the datapoints. Scenario A = Low FID and low detection; Scenario B = Low FID and high detection; Scenario C = High FID and low detection; Scenario D = High FID and high detection

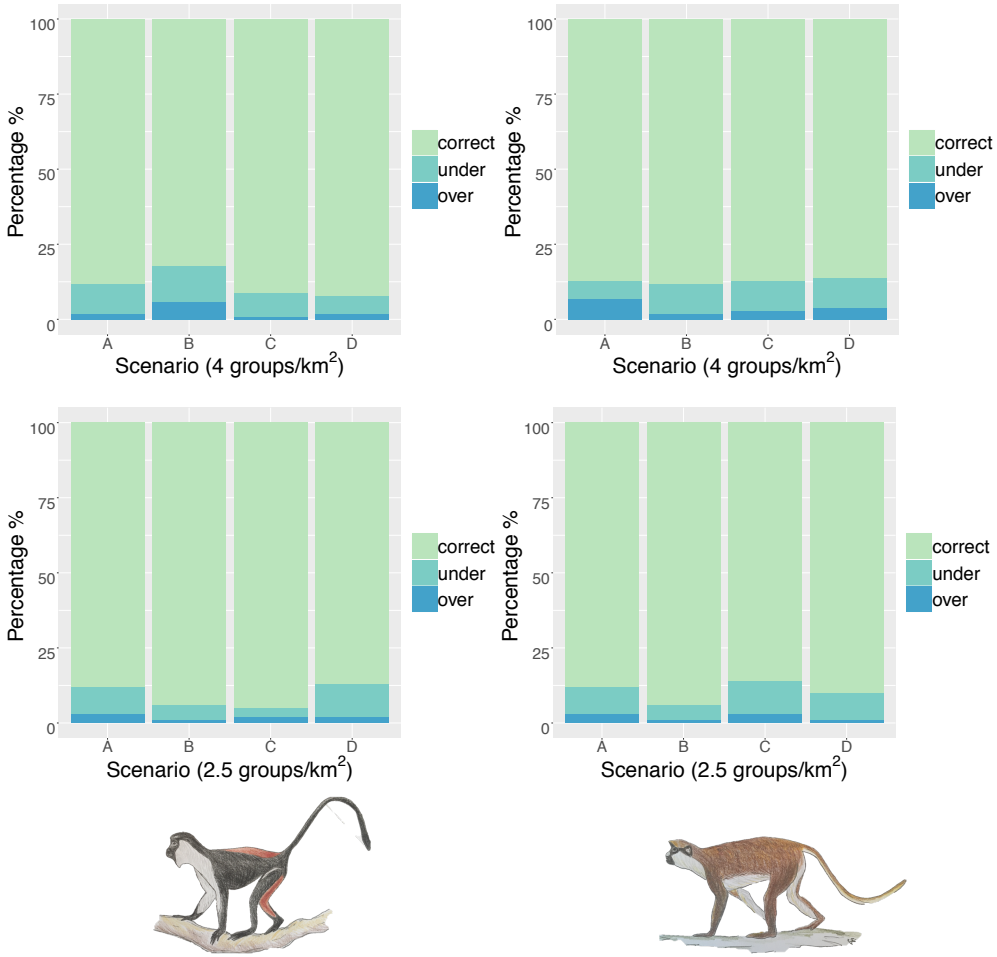

Figure 6.5 Percentage of iterations where the 95% confidence interval of the estimated density includes the actual density (correct), where the 95% confidence interval is below the actual density (under) and where the 95% confidence interval is above the actual density (over). Scenario A = Low FID and low detection; Scenario B = Low FID and high detection; Scenario C = High FID and low detection; Scenario D = High FID and high detection

Density estimates were sensitive to changes in observer step length, with longer steps resulting in lower density estimates (Figure 6.6). However, the change in observer step length did not affect differences in density estimates between the different hunting scenarios. Longer observer step length resulted in a 32% and 30% increase in iterations that underestimated density under the "low hunting" (Scenario A) and the "high hunting" (Scenario D) scenarios respectively, compared to the baseline parameter step length (Figure 6.7). Shorter step length resulted in a 1% and 5% increase in iterations that overestimated density under the "low hunting" (Scenario A) and the "high hunting" (Scenario D) scenarios respectively, compared to the baseline parameter step length (Figure 6.7).

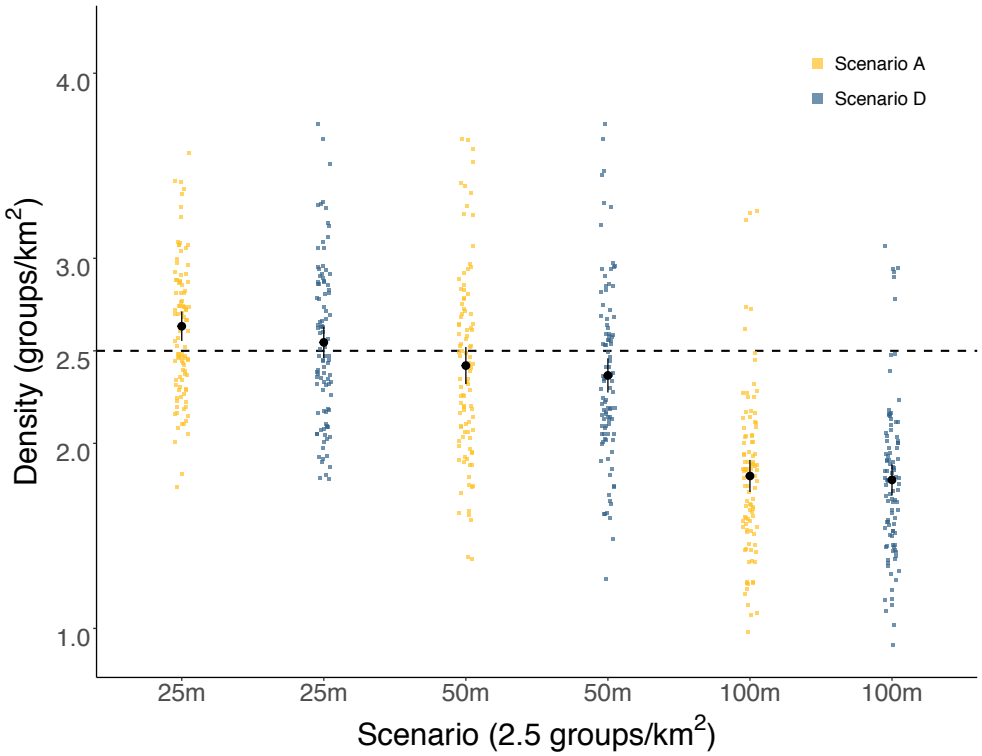

Figure 6.6 Effect of changing the observer step length (25m, 50m or 100m) along transect lines on final density estimates. Sensitivity analysis was run under "low hunting" Scenario A and "high hunting" Scenario D for Diana monkeys with a starting density of 2.5 groups/km^2

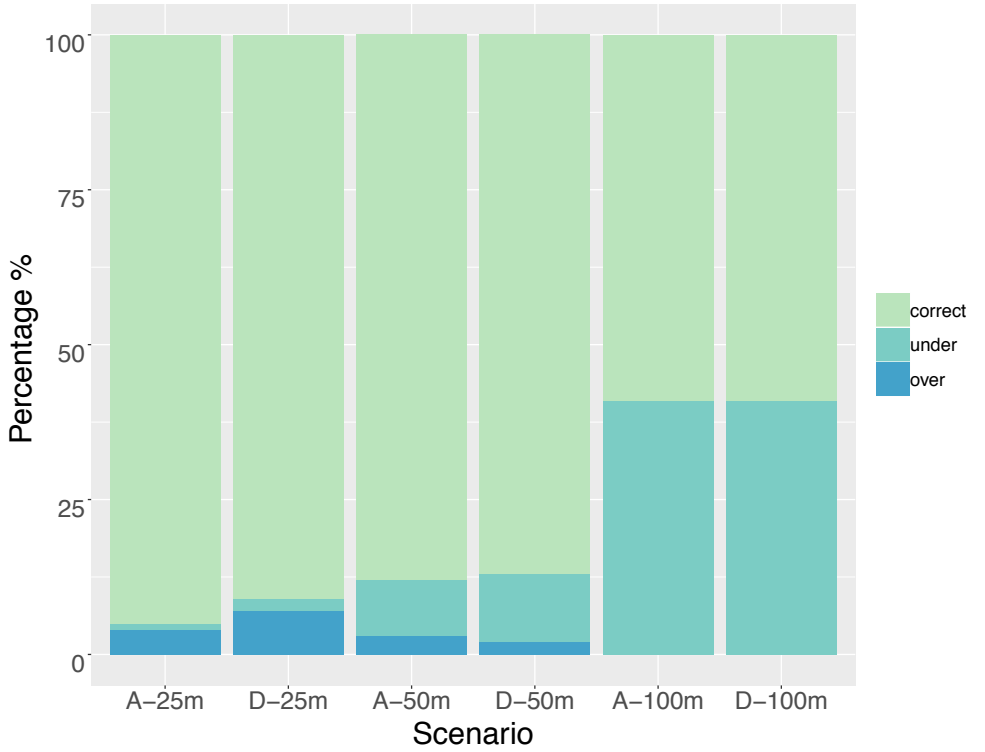

Figure 6.7 Effect of changing the observer step length (25m, 50m or 100m) on percent of iterations where the 95% confidence interval of the estimated density includes the actual density (correct), where the 95% confidence interval is below the actual density (under) and where the 95% confidence interval is above the actual density (over). Sensitivity analysis was run under "low hunting" Scenario A and "high hunting" Scenario D for Diana monkeys with a starting density of 2.5 groups/km^2

Density estimates were also sensitive to changes in monkey group mean fleeing speed, with higher speed resulting in lower density estimates (Figure 6.8). The change in mean fleeing speed did not affect the difference in density estimates between the different hunting scenarios. Higher mean fleeing speed resulted in a 2% and 5% increase in iterations that underestimated density under the "low hunting" (Scenario A) and the "high hunting" (Scenario D) scenarios respectively, compared to the baseline parameter fleeing speed (Figure 6.9). Lower mean fleeing speed resulted in a 1% increase in iterations

that overestimated density across both scenarios, compared to the baseline parameter fleeing speed (Figure 6.9).

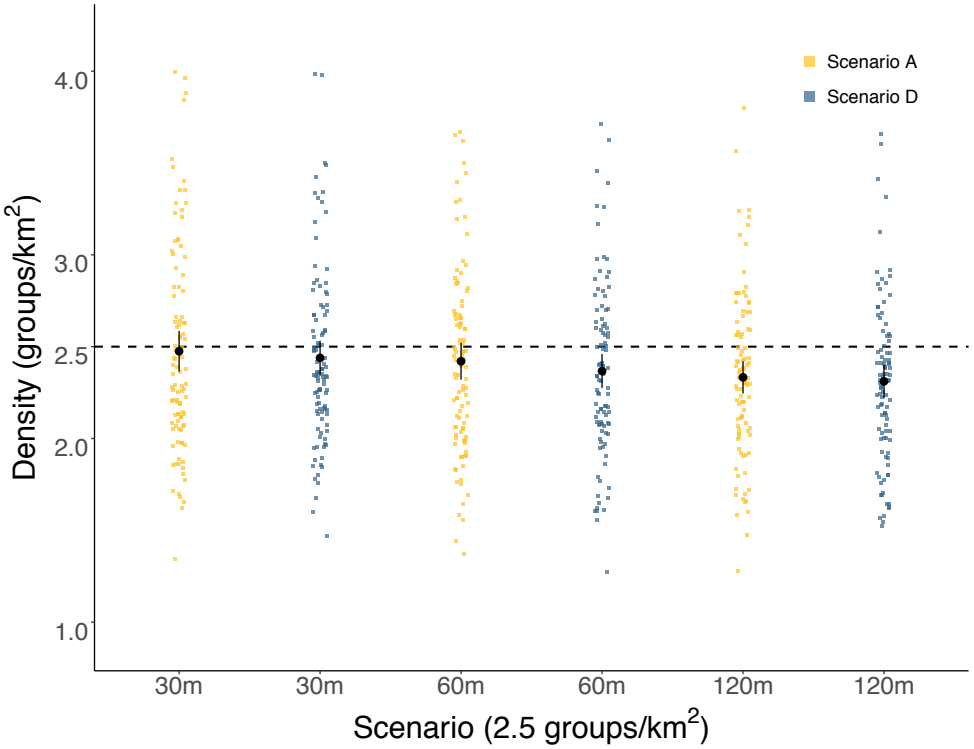

Figure 6.8 Effect of changing monkey group mean fleeing speed (30m, 60m or 120m) on final density estimates. Sensitivity analysis was run under "low hunting" Scenario A and "high hunting" Scenario D for Diana monkeys with a starting density of 2.5 groups/km^2

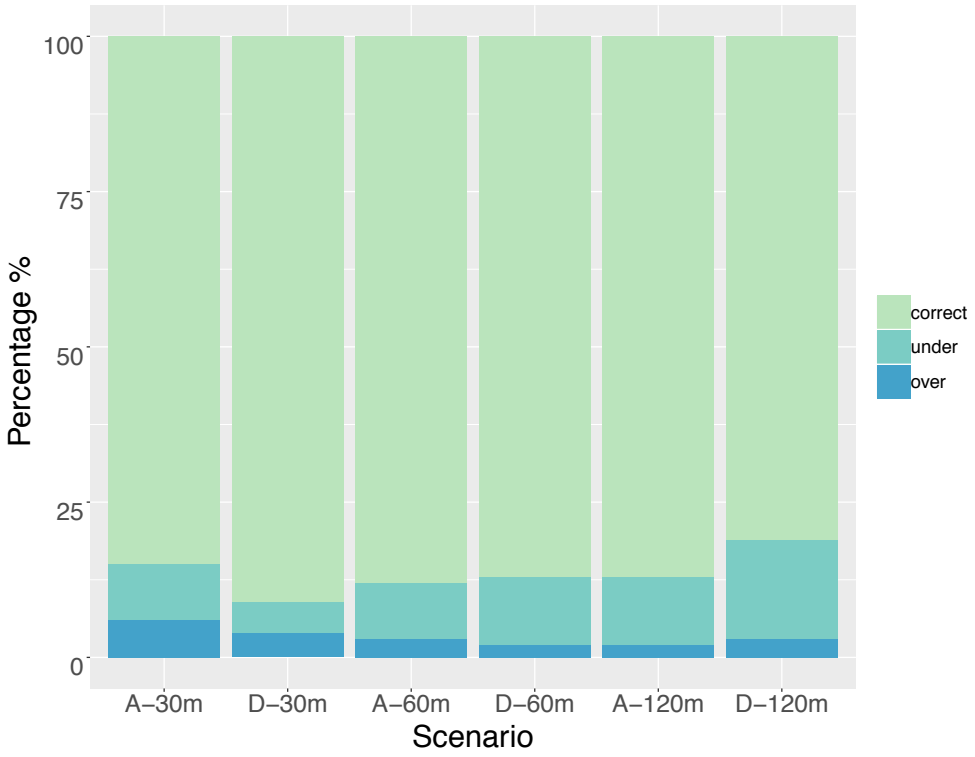

Figure 6.9 Effect of changing monkey group mean fleeing speed (30m, 60m or 120m) on percent of iterations where the 95% confidence interval of the estimated density includes the actual density (correct), where the 95% confidence interval is below the actual density (under) and where the 95% confidence interval is above the actual density (over). Sensitivity analysis was run under "low hunting" Scenario A and "high hunting" Scenario D for Diana monkeys with a starting density of 2.5 groups/km^2

6.4 Discussion

Using an agent-based modelling approach, this study aimed to explore the potential effects of variation in behaviour linked to hunting on density estimates of monkey populations. As vulnerable to hunting, the Diana monkey and the lesser spot-nosed monkey were ideal candidates to explore this potential interaction. The model simulated the behaviour of an observer walking line transects in a tropical forest to estimate the density of monkey groups. Monkey group behaviour was varied according to hunting intensity. Since longer FIDs and a greater detection ability are more likely to result in responsive movement by monkeys prior to detection by the observer, density estimates were expected to be biased lower (Buckland et al. 2001) in the scenario where the pressure from human hunting was higher. Although in all cases the density estimates were lower in the "high hunting" scenario compared to the "low hunting" one, no significant differences in density estimates were found between the different scenarios. This result is surprising, given the expectation that longer FIDs and a better monkey group detection function may violate the assumption that individuals do not move in response to surveyors prior to being detected (Thomas et al. 2010).

There are multiple potential reasons why no differences in density estimates were recorded between the different scenarios. Firstly, although significantly different patterns of FID were recorded between areas under different levels of hunting pressure (see Chapter 5, *5.3.1 Flight initiation distance (FID)*), these differences may not be large enough to result in a reduced probability

of detection. If changes in FID are not large enough to reduce detection probabilities, the fitted distance sampling detection function will likely compensate for the change in distribution of the observed perpendicular distances. Furthermore, the monkey group detection functions were parameterised from empirical observations and, although median reaction distances coincided with a 50% probability of detection, in the high hunting areas there may be a larger proportion of monkey groups that are undetected, since groups may detect and react to the observer at larger distances compared to the low hunting areas. Secondly, since many of the parameters were sampled from a distribution, the variation in parameter selection at each iteration may be partly responsible for greater variation and a lack of clear differences between scenarios.

Thirdly, there are many other behaviours that may simultaneously influence detectability and cause distance sampling assumptions to be violated. The consequent probability of detection is likely a function of the interaction between these multiple behavioural factors. Since the model is quite simple and only includes variation in FID and the monkey group detection function, it could be that it does not capture other aspects of avoidance behaviour that influence the probability of detection. Fleeing speed, for example, could vary with hunting pressure and could potentially have a greater impact on the assumption of "no movement prior to detection by the observer" than FID. The model has potential for other empirically observed behaviours, such as vocalisation rate and freezing, to be incorporated. This could be achieved, for example, by including different observer detection functions for animals

detected through sight and for ones detected through vocalisation, with varying probability of monkey group vocalisation. Furthermore, freezing behaviours likely result in reduced likelihood of detection on the transect, since a tropical forest habitat provides ample shelter for animals to hide effectively and pass completely undetected (Caro et al. 2004). It is thus very difficult to collect data on freezing probabilities, since a large number of groups go undetected because of it. Including these behavioural patterns would likely increase the difference in resulting density estimates between areas under different levels of hunting pressure.

Despite no clear evidence of an effect of behaviour on density estimates, since the trend is in the expected direction, this suggests that with additional empirically informed behavioural data, the differences may become more evident. There is some evidence that a reduction in call rate and an increase in freezing behaviour reduce detectability and density estimates. In Indonesia, for example, estimates from periods of low vocalisation underestimated densities of rainforest Galliformes by 13-20% compared to densities from periods when the animals were more vocal (Nijman 2007). Following logging in a forestry concession in West Malaysia, the number of primate groups seen decreased by 25%, despite the same number of groups being present (Johns 1985). The decrease in detectability was due to an increase in cryptic behaviours; after logging there was a reduction in fleeing behaviour and call rate and an increase in freezing behaviour, with primates becoming generally more inactive given the change in distribution of their food supply (Johns 1985). This further suggests that the effect on detectability may be additive,

with multiple behavioural changes having an overall effect on detection probability.

A limitation of the model is having the group as a single entity, since group size is another factor that likely affects detectability on the line (Buckland et al. 2010). As seen in Chapters 4 and 5, larger groups are generally noisier (*4.3.5 Vocalisation*), slower to flee (*5.3.2 Fleeing time*), more likely to inspect (*5.3.3 Inspection*), and therefore likely more detectable. Since group size decreases with hunting pressure (*4.3.1 Group size*), areas under high hunting may contain a bigger proportion of smaller, less detectable groups, which may further impact density estimates. I highlight this as an important avenue for further research.

The sensitivity of the model to the number of observer steps is not surprising. When step length is longer, some groups are likely missed, violating the assumption of certain detection on the line. Therefore, there is likely to be a relationship between step length and density estimates. Since this modelling caveat did not have an effect on the difference between hunting scenarios it was not considered a particular issue. Furthermore, the chosen baseline step length resulted in fairly accurate density estimates. It was surprising that monkey group fleeing speed did not have a bigger effect on overall density. Since monkey group speed was parameterised from another field study, the distribution of monkey group fleeing speeds may not be large enough to affect detection probabilities significantly.

The first essential step to protect animal populations from the ever-impending threat of human expansion and exploitation is to effectively monitor population numbers and estimate densities correctly. Given the high threat that human hunting pressure poses for many animals worldwide, it is crucial that this effect is accurately monitored (Bawa and Menon 1997). Accurate density estimates allow to measure population change, evaluate hunting sustainability and assess the effectiveness of conservation interventions. When estimating animal densities under threat from human hunting, it is important to understand behavioural plasticity in relation to census methods (Sutherland 1998; Nijman 2007), as this could lead to a violation of distance sampling assumptions and affect detection probabilities (Johns 1985).

Agent based models can be a promising tool to model true behaviours (Dobson et al. 2019b). This model is a first step to implement an approach based on modelling from empirically collected behavioural data. Since there is no way of knowing the true density in a natural habitat, a modelling approach allows to simulate the census process and provides a first understanding of the potential magnitude of the bias. Despite not showing the expected differences in density estimates, this model still provides a first insight into an approach to quantify the potential effect of avoidance behaviour on density estimates. Given the accurate estimates produced, which closely reflect model inputs of density, this model provides a good baseline to investigate potential biases of other behaviours or other species. Once expanded with other behavioural parameters, this framework has the potential to be turned into a user-friendly application, where the user inserts species-

specific empirical data and the output provides guidance towards the extent of the effect of that behaviour on density estimates. It would be interesting to build a library of different behaviours to establish conceivable interspecific differences in density estimates as a result of behavioural differences between species, since some species are naturally more cryptic than others. Given the difficulty in collecting accurate behavioural data both under high hunting conditions and in tropical forest habitats it may not always be straightforward to parameterise the model for other species. However, a robust and well-designed study on a particular species may provide valuable empirical data that can then be used for model parameterisation and potentially inform patterns elsewhere.

Chapter 7

Discussion

A first step to safeguard the planet's invaluable biodiversity from human pressures such as hunting, is to understand the precise spatio-temporal dynamics of the threat and to accurately measure the consequences this may have on species, communities and ecosystems (Balmford et al. 2005; IUCN 2012). How can we identify accurate IUCN (International Union for Conservation of Nature) Red List categories for species if we don't know the extent of the threat and how this affects their numbers and behaviour? The main aim of this PhD was to investigate the effect that different spatial indicators of hunting pressure have on the resulting predicted distribution of hunting, how these pressures relate to behavioural change in monkeys and finally whether this change affects the accuracy of density estimates. The results showed 1) that indicator chosen does impact the predicted spatial distribution of hunting, 2) that certain behaviours do vary with hunting pressure, but some indicators of hunting better predict behavioural change compared to others, and 3) that, at least when modelled separately, variation in measured behaviours does not affect density estimates. This chapter summarises these results, emphasising their value for conservation and suggesting potential avenues for further research.

7.1 Hunting pressure indicators

Knowing the spatial distribution of hunting is important in order to predict its effect on both target and non-target species and to implement tailored conservation action (Fa et al. 2005). By mapping the locations of hunting hotspots within a forest, for example, we can begin to understand how species react to this pressure and which areas to focus conservation efforts on. Methods to estimate hunting pressure can vary from fine to broad spatial scales, capture temporal "snapshots" of hunting or use indirect proxies to infer hunting distribution. A comparison to understand and quantitively assess the extent of the difference was missing. Despite an array of methods being used to estimate the distribution of hunting pressure, this was the first study to compare and evaluate different indicators, by highlighting costs and benefits of each one and suggesting their appropriate use under different research objectives (Chapter 3).

Chapter 3 addressed this knowledge gap by comparing hunting maps built using different indicators: 1) distance from human settlements, as hunting distribution is assumed to decrease with distance from human infrastructure (Sirén et al. 2004; Constantino 2016), 2) encounter rate of hunting signs and 3) frequency of gunshots. These maps were then assessed with respect to the three levels of law enforcement within the region. Overall, the maps showed very different hunting pressure distributions, and each identified different law enforcement areas as having the highest level of hunting intensity. Furthermore, the results highlighted major differences in the amount of effort

involved in generating the maps (both financial and in time to collate and analyse the data). This study can thus be a useful reference for practitioners as guidance to help select a method according to the resources available. Finally, the resulting maps emphasise the varying spatial scales of the different methods. The distance map appears smooth, the hunting sign and gunshot frequency maps are much more fragmented, whereas when comparing law enforcement areas, the distribution of hunting pressure is assumed to occur in large “blocks”.

The main limitation of this study was the impossibility of collecting data simultaneously for the different maps. Given the huge effort required to gather such data, previous monitoring data was used to construct the hunting sign map. Differences in hunting distribution between maps could therefore be a reflection of temporal changes in hunting dynamics and may not entirely reflect differences between methods. Despite this being a limitation in the study, “imperfect temporal comparability” is likely often an issue for conservation projects, limited by data and resources available to them. An interesting avenue for further research would be to collect data on a yearly basis and use different methods to construct yearly map comparisons. This would help discern temporal hunting patterns from differences in hunting distribution captured by the different maps. Such a study could be carried out by park managements by incorporating data collection into ongoing monitoring schemes. Collecting for example yearly data on hunting signs alongside biodiversity surveys and adding recorder deployment to camera trap monitoring programmes, which are often already part of many

monitoring projects. Further limitations, however, may be linked to the availability of suitable expertise to analyse this type of data. Ideally, parks with a greater range of resources would be more suited for carrying out such investigations. Results could then be useful for a wide range of parks with scarcer resource availability.

Another limitation of the study was the small region and the limited recording period captured by the Audiomoth recorders. Ideally, more recorders would have been placed for a much longer period of time. This, however, would have required a huge deployment effort, out of reach for this PhD. Furthermore, limitations in processing time post-deployment further limited the realistic amount of audio data collectable. Technological advances in recorder battery life, algorithms to detect gunshots, and a reduction in cost of the devices (Hill et al. 2018; Prince et al. 2019) means future work is likely to be less limited by the issues encountered during this study.

Since it is hard to know which map is a true representation of hunting distribution, it would be interesting to validate results with data collected using other monitoring techniques. Working alongside hunters through participatory mapping techniques and hunter follows can help understand hunting practices and their true spatial dynamics (Rist et al. 2009; Coad et al. 2013). Care should be taken however, since the illegality which is often associated with hunting may lead to inaccurate reports of hunting practices (Nuno et al. 2013).

7.2 Variation in risk and antipredator behaviour

Since predation generally exerts a strong pressure on prey species (Caro 2005), it is likely that the spatial distribution of human hunting influences the avoidance behaviour of hunted species as well as their densities (Fa and Brown 2009). Behavioural change varies from baseline adaptations to minimise detection, to changes in antipredator responses, with varying impacts on the fitness of the species (Edmunds 1974). Response to predation risk is constrained by fitness thresholds that need to be met by the animals (Lima and Dill 1990), and will thus depend on the spatio-temporal variation of that risk (Lima and Bednekoff 1999; Laundré et al. 2010). Quantifying behavioural change in response to hunting can help measure the non-lethal consequences of the threat on target species (Verdade 1996; Lind and Cresswell 2005). However, compared to the vast number of studies that estimate the effect of hunting on species densities, relatively fewer studies focus on behavioural change. Furthermore, studies on primates often use a single predictor of hunting pressure and focus on a limited number of study groups, with the unhunted sample often being semi habituated to researchers (Watanabe 1981; Bshary 2001; Croes et al. 2006; Koné and Refisch 2007).

In Chapters 4 and 5, I assessed changes in Diana monkey (*Cercopithecus diana*) and lesser spot-nosed monkey (*Cercopithecus petaurista*) behaviour as a result of hunting across a large number of independent unhabituated groups and using the multiple hunting pressure indicators described in Chapter 3. I hypothesised an increase in avoidance behaviours with increasing

hunting pressure in both species, with stronger effects in Diana monkeys since the species is more vulnerable to hunting. As predicted, the results indicated that both species adapt certain behaviours to level of hunting pressure. The group size of Diana monkeys decreased with an increase in encounter rate of hunting signs, potentially highlighting the effect of hunting on numbers or perhaps suggesting fine scale local adaptations in group size. This is likely a reflection on the small group home range of this species. It would be interesting to test the same predictions on species with broader ranging patterns to understand how an animal's home range size might interact with spatial changes in hunting pressure.

Changes in flight initiation distance (FID) and fleeing times were predicted by broad scale law enforcement areas in both species. Perhaps these behavioural changes occur over longer time periods and are hard to predict with "snapshot" indicators such as encounter rate of hunting signs. With data on temporal change in hunting pressure, further research could potentially measure timescales of antipredator behavioural change to understand how exposure to hunting pressure changes behaviour over time. Not all of the tested behaviours were affected by hunting. Perhaps detailed data on resource availability and a better understanding of the spatial distribution of other predators might help discern observed variation in other behavioural variables. Furthermore, differences in behavioural response may also be linked to individual variation, with fitter animals that live in more suitable habitats being able to better invest in antipredator responses (Spitz et al 2019). It would be extremely challenging however to gather data on the fitness status

of different groups, since hunting threat means it is very difficult to observe groups close by.

The results of this study have implications for the fitness of both Diana monkeys and lesser spot-nosed monkeys, and consequent wider implications for their conservation. The fact that monkeys are fleeing at larger distances in areas with more hunting, for example, suggests that they are more vigilant in those areas, thus taking time away from fitness enhancing activities. Hunted species therefore not only face the threat of reduced population sizes but are likely suffering from reduced fitness associated with fear and less time spent feeding and mating. There is evidence that perceived predation risk can have significant effects on reproductive output (Lind and Cresswell 2005). Grey-sided voles, *Clethrionomys rufocanus*, for example, significantly reduced their breeding when subject to a predator odour (Fuelling and Halle 2004). Wolf spiders, *Paradosa milvina*, that exhibited predator avoidance behaviours, produced egg sacs that were lighter in weight and a reduced number of eggs (Persons 2002). Thus, though hard to measure, it is not unreasonable to suggest that the recorded avoidance behaviours in these species may translate into broader fitness costs. Furthermore, since detectability is negatively affected by elusive behaviour, density estimates of hunted species may likely underestimate species numbers.

7.3 Detectability and density estimates

Supporting some previous research (Watanabe 1981; Bshary 2001; Croes et al. 2006), Chapters 4 and 5 highlight changes in antipredator behaviours in primates as a result of exposure to human hunting pressure. Since these changes in behaviour are likely to render species less detectable to researchers as well as hunters, and thus may lead to violations in distance sampling assumptions, these trends could potentially lead to underestimates of densities in areas where hunting occurs. A species may therefore be deemed unsustainably hunted and conservation measures may be implemented accordingly. It could be instead that for some species, densities in hunted regions are similar to those in unhunted regions and the resulting differences in density estimates are due to adaptations in avoidance behaviour. Given the valuable resource that wildmeat represents for people in many tropical regions, it is important to accurately estimate hunting sustainability of different species.

Since it is impossible to validate density estimates of forest dwelling primates against their true densities, in order to understand the potential impact of behaviour on density estimates, agent-based modelling can provide a useful tool to simulate interactions and outcomes given a set of behaviours. This approach, however, had not yet been implemented. In Chapter 6 I modelled the effects of some of the behavioural covariates measured in Chapter 5 on density estimates of Diana monkeys and lesser-spot nosed monkeys, using an agent-based modelling approach. Contrary to expectations, model results

suggested that changes in FID and monkey detection function do not significantly affect final density estimates of these species, although density estimates were consistently lower in the “high hunting” scenario compared to the “low hunting” one. Perhaps each individual behaviour has a small effect, but multiple behavioural changes could lead to an additive effect, such that behavioural differences would have an impact overall. Future research could build this model by adding other behavioural variables, such as differences in fleeing time, to measure whether the combined effects of different behaviours leads to underestimates in density. Furthermore, it would be valuable to test this modelling approach across different species with varying behavioural responses to hunting, to build a comparative assessment of interspecific differences in behavioural effects on density estimates.

If adding other behavioural variables through further modelling does not affect the resulting density estimates, it may be that, at least for these species, it is not necessary to incorporate variation in behaviour linked to hunting in density estimate calculations, since this has little effect on the overall accuracy of the estimations. If, on the other hand, the difference in density estimates increases significantly with additional behaviours, including behaviour in density estimations would likely become very important and could highlight potential underestimates of densities in hunted regions so far. This would potentially have broader implications for sustainability estimates of these species and others with similar antipredator behavioural patterns.

7.4 Conclusion

Anthropogenic hunting pressure may have marked effects on species. Without a true understanding of the interactions between hunting and the corresponding biological systems affected, it is impossible to implement targeted conservation measures. This PhD thesis investigates these issues firstly by evaluating hunting maps and highlighting that indicator chosen does impact the predicted spatial distribution of hunting; secondly by quantifying the effects of hunting on behavioural change in primates and finding that certain behaviours do vary with hunting pressure, but some indicators of hunting better predict behavioural change compared to others; thirdly by linking behaviour to density estimates and emphasising that, at least when modelled separately, variation in measured behaviours does not affect density estimates. Even though this study tackles these themes through a case study of monkeys in a West African forest, as highlighted above the results have broader conservation implications for wildlife across tropical systems. This study reminds us of the importance in focussing conservation efforts on the study of behaviour and emphasises its relevance for conservation.

Appendix 1

PCA analysis

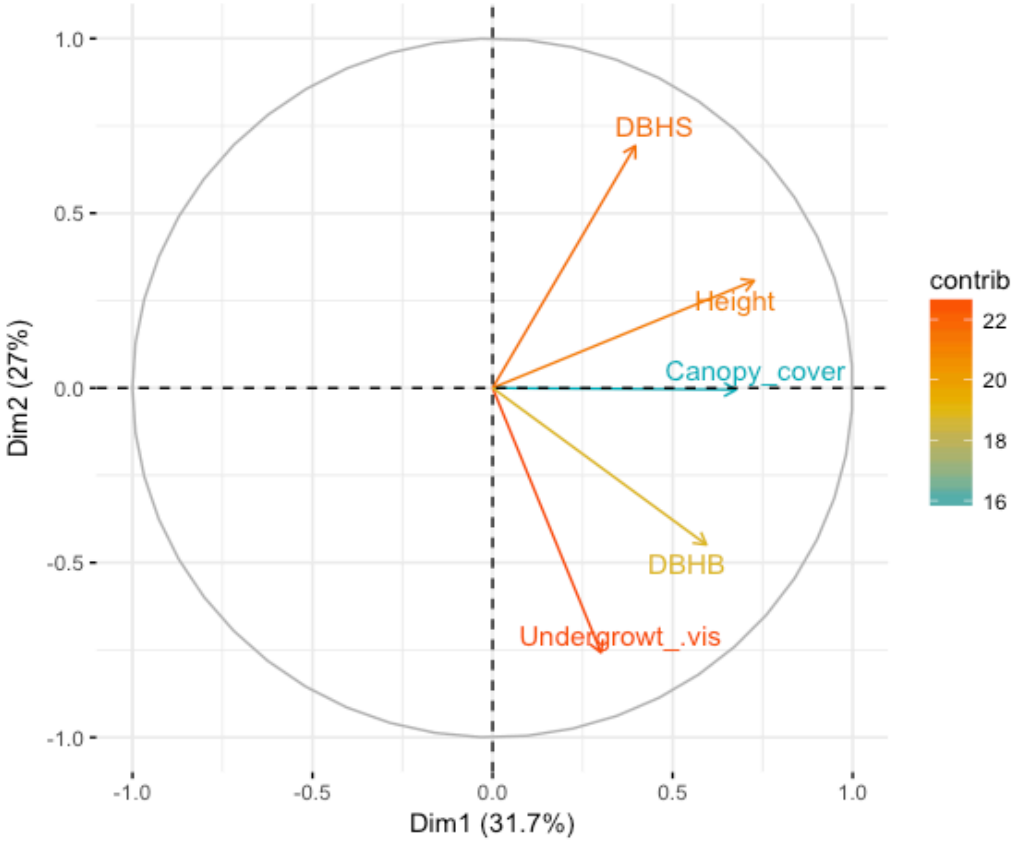

Figure A1.1 Biblot showing main PC axes linked to habitat variables. PC1 and PC2 cumulatively explain 58.7% of the variation. Canopy cover = % canopy cover, height = mean tree height, undergrowth_vis = % undergrowth visibility, DBHS = number of small trees with diameter at breast height (DBH) between 1-10 cm, DBHB = number of large trees with DBH greater than 30 cm.

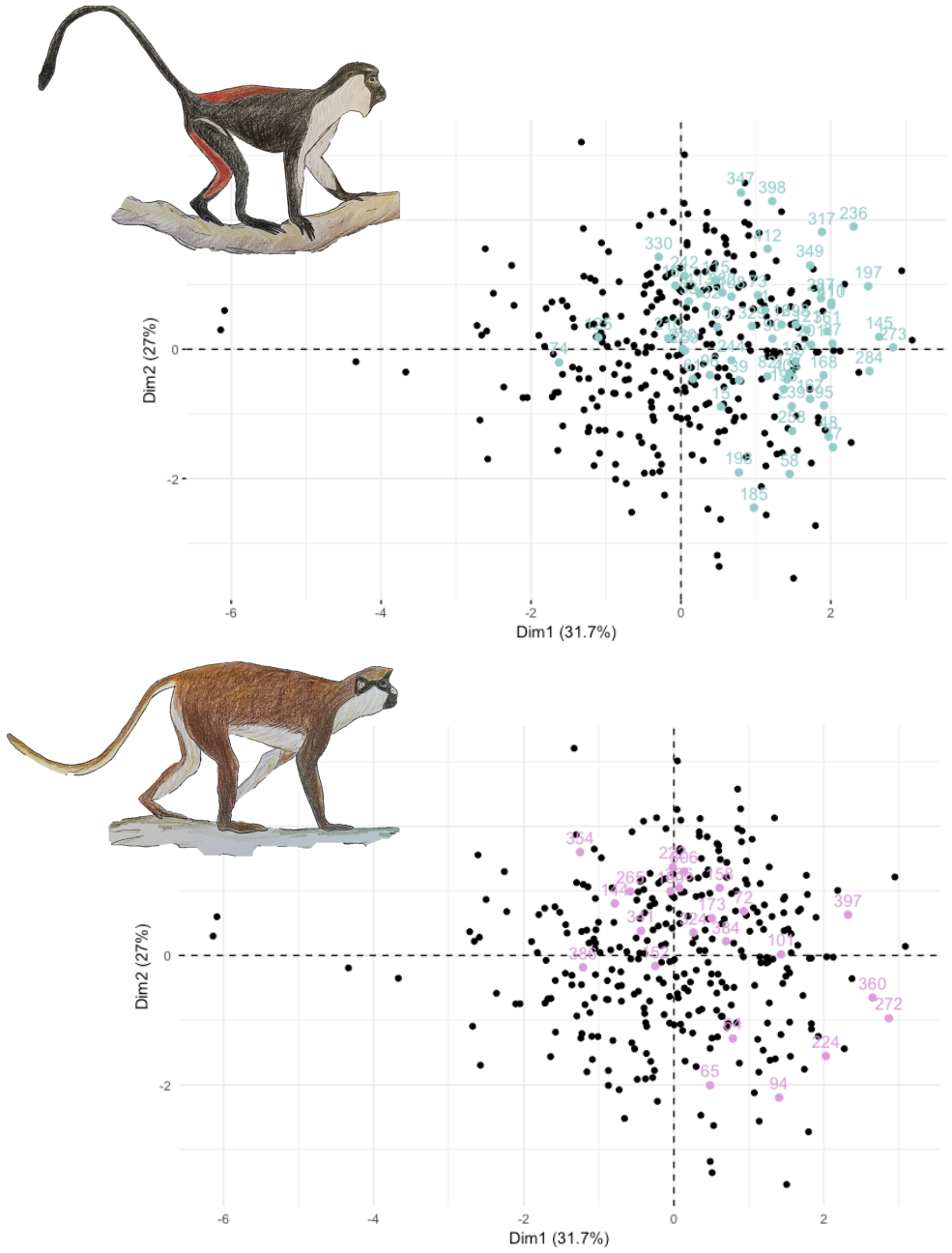

Figure A1.2 Species specific habitat preferences are evident from the clusters formed by the monkey-level habitat plots added to the PCA. Diana monkey habitat plots cluster to the positive side of axis 1: on average taller trees with greater canopy cover and higher numbers of bigger trees (i.e. primary/degraded primary forest). Lesser spot-nosed monkey habitat plots cluster mainly to the positive side of Axis 2 (although more variation is present for this species): on average higher number of smaller trees and lower undergrowth visibility (i.e. secondary forest)

Appendix 2

Hunting pressure maps

Scanning of the literature

To review the literature on methods used to measure hunting pattern distribution, all issues within five main conservation journals published over the past 10 years were scanned (2009-2019). The chosen journals were Biodiversity and Conservation, Biological Conservation, Biotropica, Conservation Biology and Oryx. These journals were selected given the high prevalence of published literature on hunting. Titles were scanned for all papers which may contain a spatially explicit measure of hunting pressure. These may include any papers looking at the effect of anthropogenic pressures on species numbers, interactions or behaviours (which may contain a measure of hunting), any papers evaluating the effectiveness of project interventions and papers looking directly at hunting pressure indicators. If it was unclear from the title whether hunting pressure was measured, abstracts were scanned for further information. Abstracts of the selected papers were then read to decide whether the appropriate measure was recorded. Hunting pressure methods used were subsequently extracted from the remaining papers. These were then grouped into the 10 methods found in Figure 3.1. Acoustic recording methods were not found during this scanning process but were included in the diagram as this was one of the methods used in the current study.

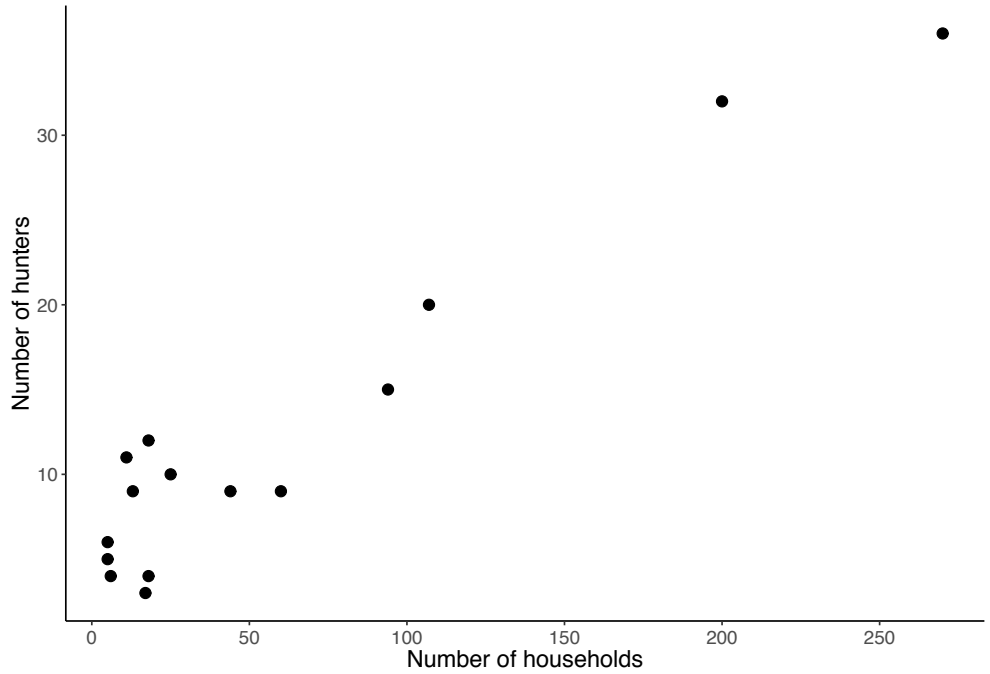

Figure A2.1 Positive correlation between number of households and number of hunters in the communities participating in the GolaMa project (Spearman's rank correlation, rho=0.74, S= 146.92, n=15, p=0.002)

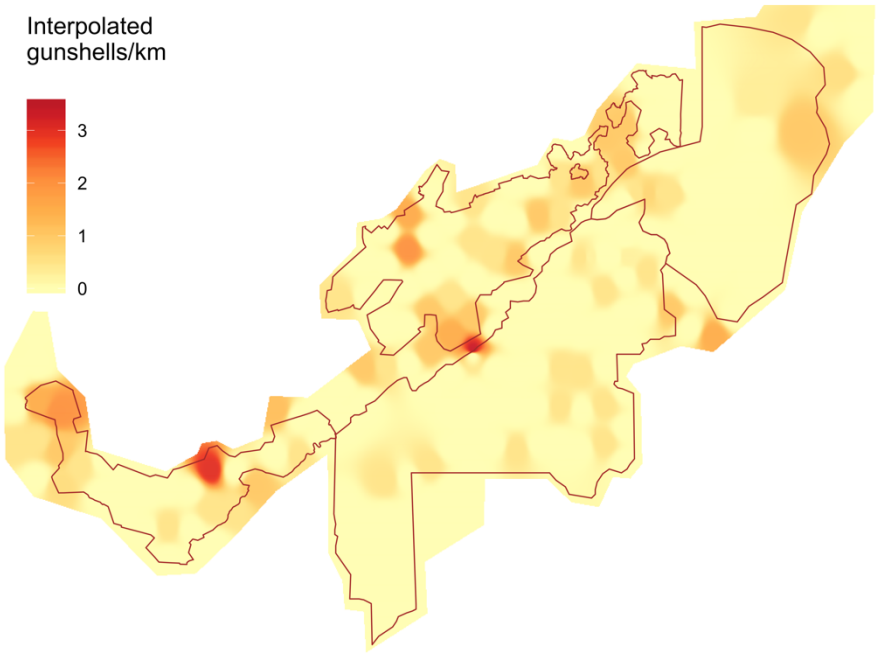

Figure A2.2 Map of hunting pressure derived using inverse distance weighted interpolation from encounter rates of empty gun shells per km

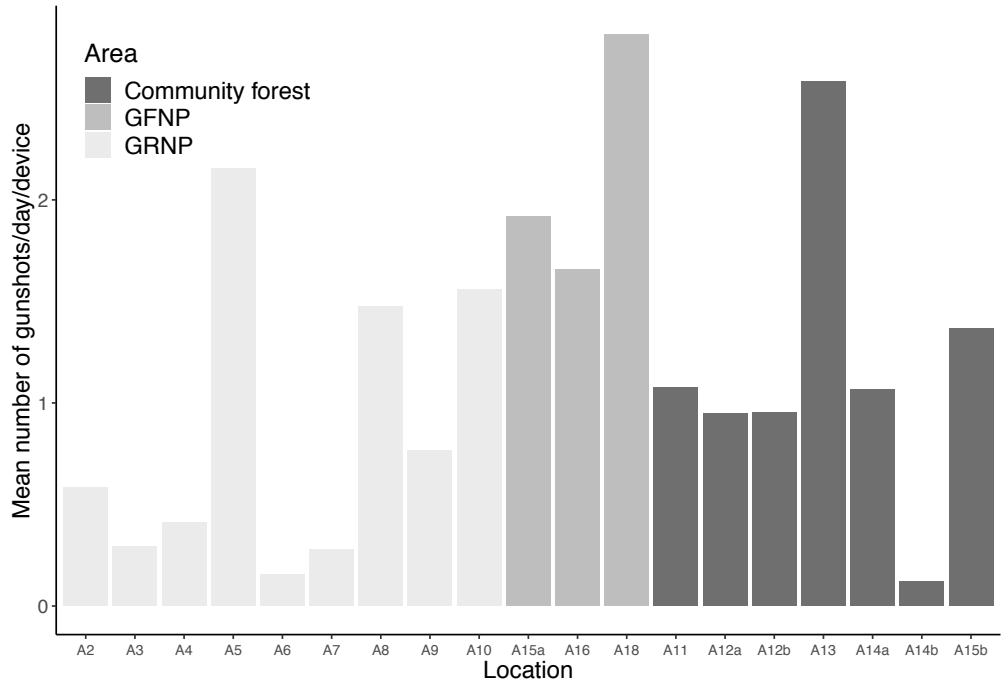

Figure A2.3 Mean number of gunshots per day, per device, as recorded at 19 locations and split according to level of law enforcement. Community forest: GolaMA project community management area (Liberia), GFNP: Gola Forest National Park (Liberia), GRNP: Gola Rainforest National Park (Sierra Leone**)**

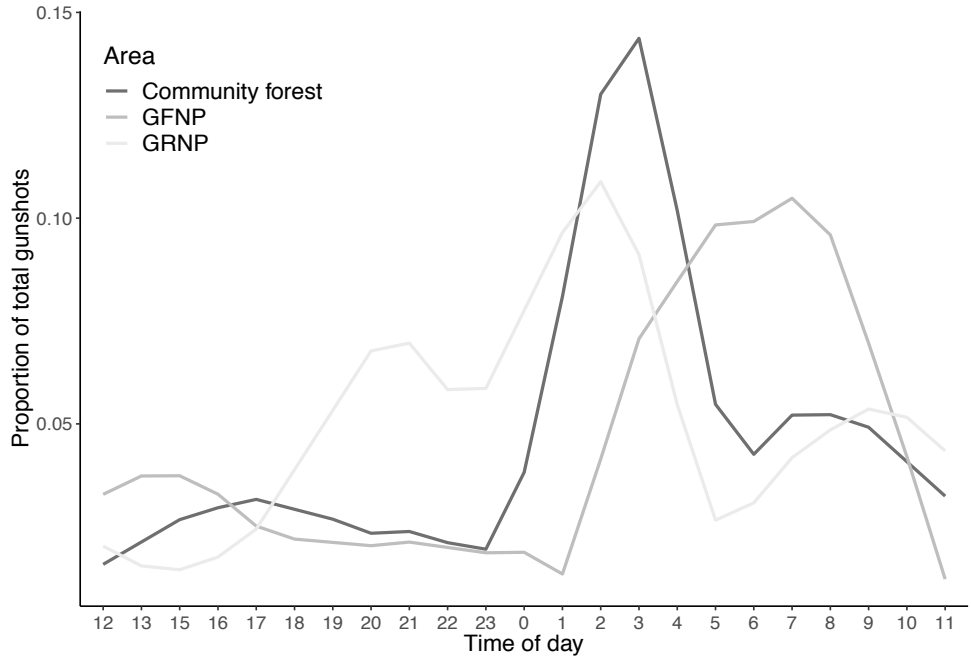

Figure A2.4 Proportion of gunshots recorded at different times of day (24-hour clock) and split according to level of law enforcement. Community forest: GolaMA project community management area (Liberia), GFNP: Gola Forest National Park (Liberia), GRNP: Gola Rainforest National Park (Sierra Leone**)**

Appendix 3

Primate Behaviours

Table A3.1 Sample size, mean and standard deviation for each behaviour of other primate species recorded in Gola

Behaviour	**Campbell's monkey (n=9)**	**Sooty mangabey (n=14)**	**Red colobus (n=11)**
Height in trees (m)	21.42 ± 10.79	7.80 ± 13.17	35.27 ± 2.46
Group size (individuals)	4.89 ± 4.23	4.86 ± 2.74	24.55 ± 11.36
Visibility before detection	0.63 ± 0.66	1.09 ± 1.58	5.91 ± 5.13
Change in visibility	0.72 ± 1.11	0.48 ± 2.89	0.41 ±0.90
Flight Initiation Distance (m)	40.89 ± 13.85	25.79 ± 7.39	27.64 ± 6.55
Fleeing time (minutes)	5.78 ± 5.70	3.07 ± 4.68	12.91 ± 10.17
Probability of inspection	0.56	0.57	0.73

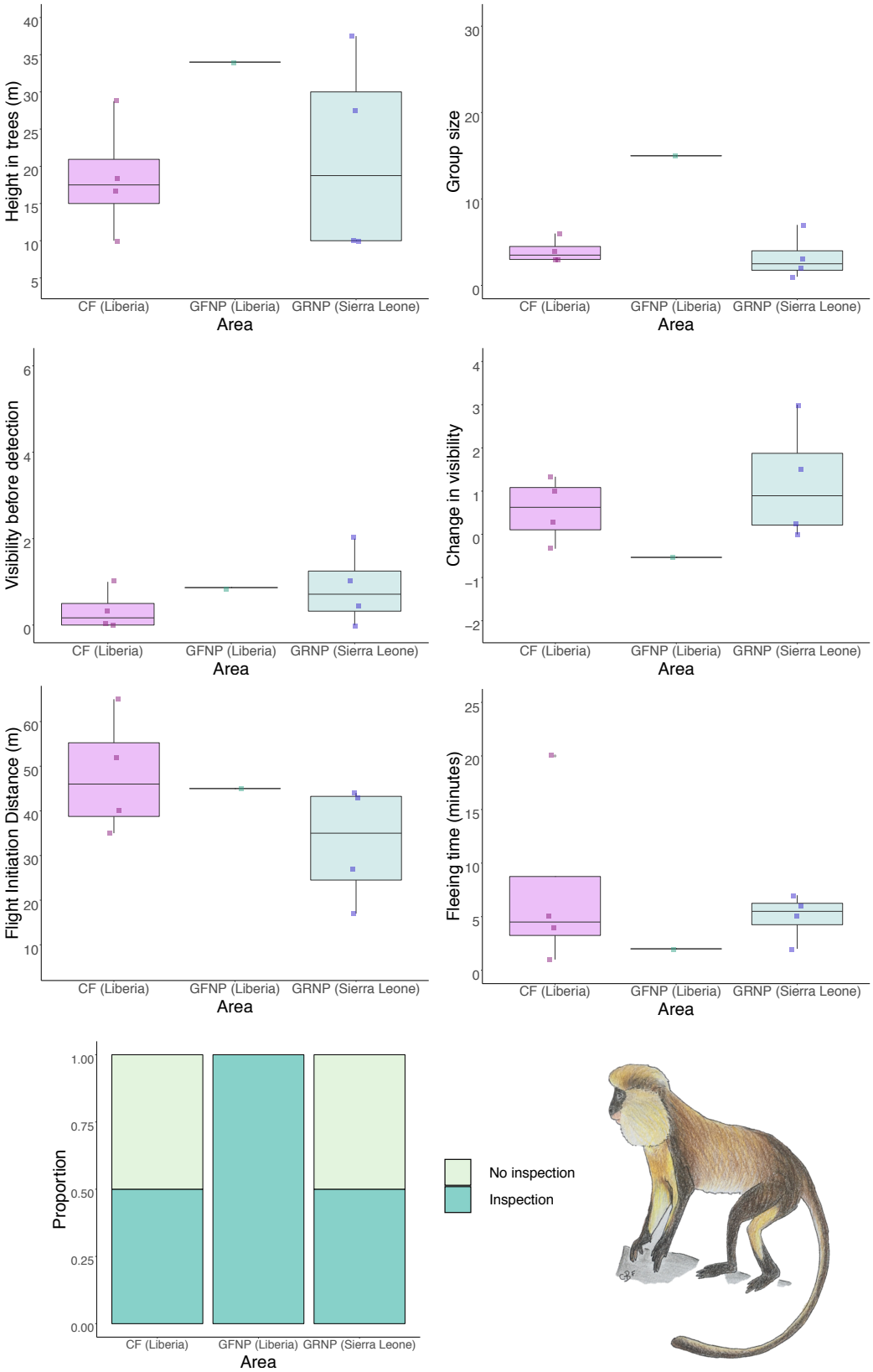

Figure A3.1 Campbell's monkey - *Cercopithecus campbelli.* Box plots show first quartile, median and third quartile, vertical lines show ranges excluding outliers, dots show the raw data

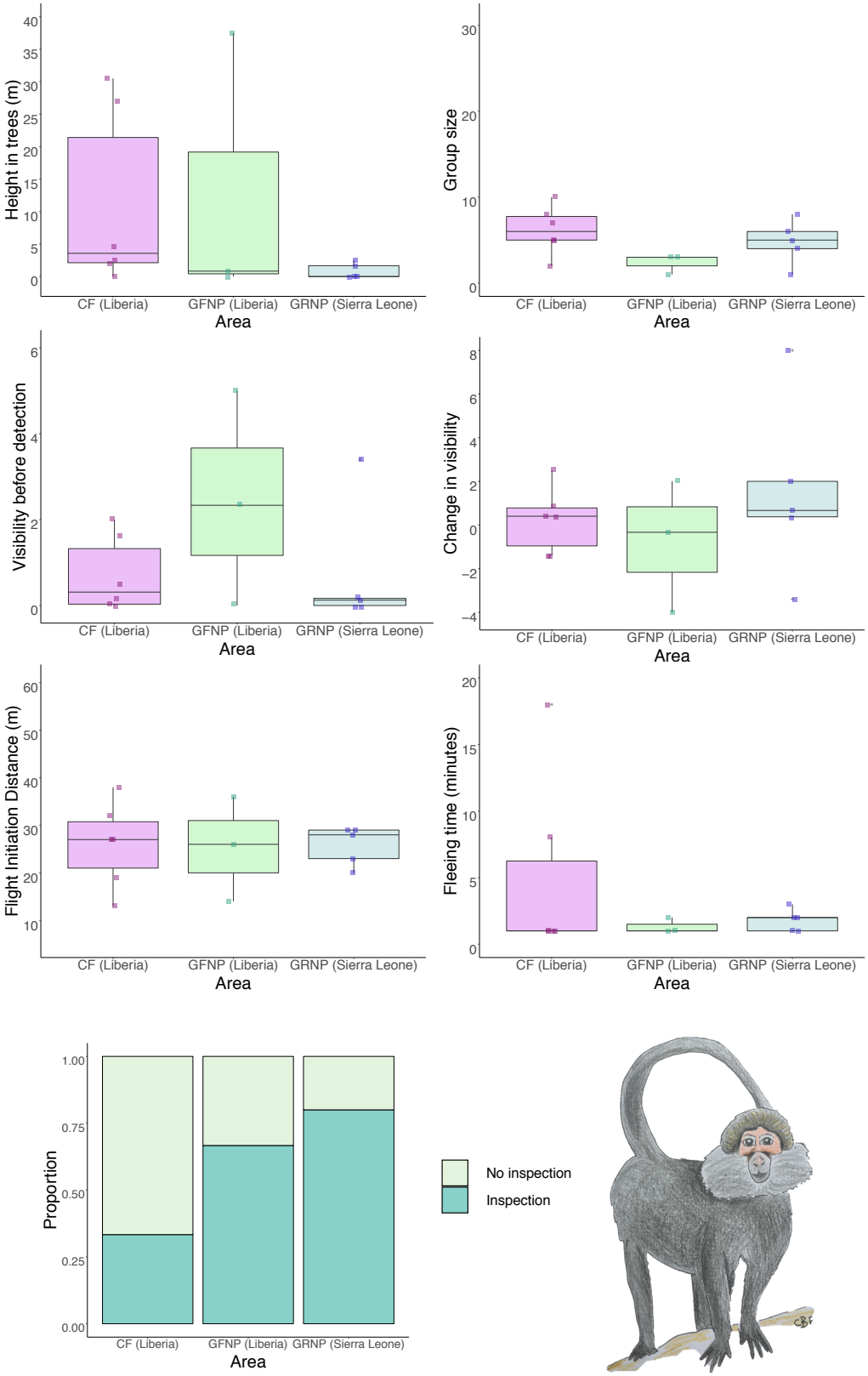

Figure A3.2 Sooty mangabey - *Cercocebus atys.* Box plots show first quartile, median and third quartile, vertical lines show ranges excluding outliers, dots show the raw data

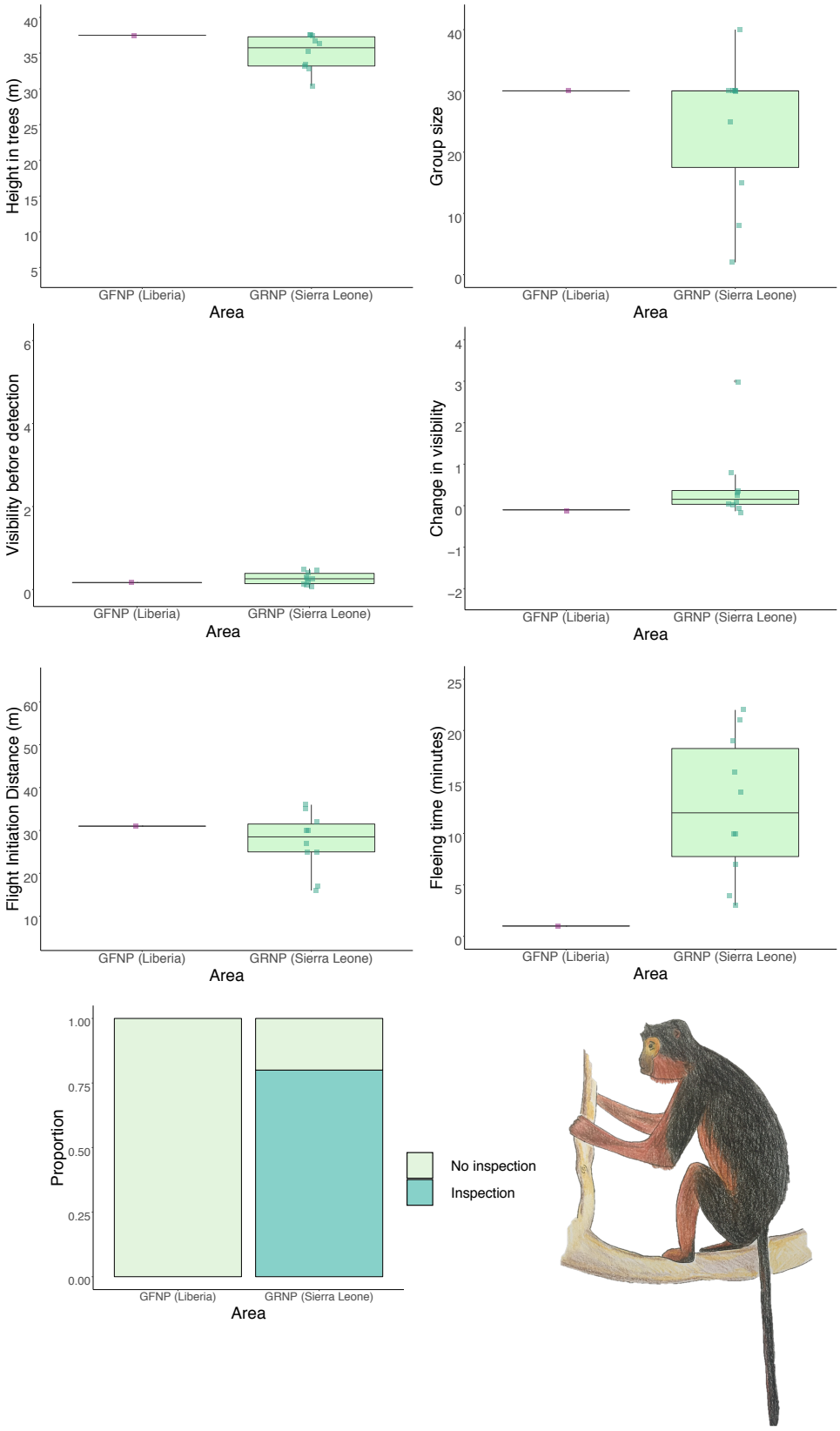

Figure A3.3 Red colobus monkey - *Piliocolobus badius.* Box plots show first quartile, median and third quartile, vertical lines show ranges excluding outliers, dots show the raw data

Appendix 4

Model code

 # final model function

```
# model

# define model parameters
model = function (

  grid.size.x = 147500,
  grid.size.y = 9000,
  monk_density_grp_km_2 = 2.5, #set number of monkeys
  numtransects = 60, #number of transects
  numsteps = 200, #how many steps from start to finish (number of steps)
  plot_monk = F,  #plot at the end: yes or no
  plot_video_slides = F , #output plots saved to selected folder
  video.name = "third.vid", #name of ouput file
  scale.param = 27 ,#affects how quickly probability of detection falls
  shape.param = 2 ,#affects the shape of the detection function
  fid.param = NULL ,#distance at which monkeys run away (from my data).
Sampled from vector of numbers
  monk.scale.param = 30, #affects how quickly probability of detection falls
  monk.shape.param = 3, #affects the shape of the detection function
  kappa = 50, #how narrow is the von mises distribution (higher kappa,
narrower the distribution)
  speed.dist.rate.decay = 0.15, # baseline monkey speed
  norm.mean = 60 # monkey speed when detected

)
```

```
 #######

 # SCRIPT

 #######


{
 # Density = num monkey groups
 num.monkey.grps = round( monk_density_grp_km_2 * ((grid.size.x/1000)
* (grid.size.y /1000)))

 # Video
 if( plot_video_slides){
  video.folder = file.path( PROJHOME, "Figures" , video.name) # PROJHOME
is a code found in the main folder (monkeyMAD).
  if( !file.exists(video.folder) ){
   dir.create(video.folder)
  }
  pdf( file.path( video.folder, paste0(video.name,".pdf") ))
 }

 # Cami's trajectory
 camwalk = camwalk.funct(numsteps, numtransects = numtransects,
grid.size.x = grid.size.x , grid.size.y = grid.size.y)
 start.new.transect = c(0,which( diff(camwalk["x"]) != 0))+1


 {
  #make a loop: for each row (nrow) in camwalk dataframe - repeat, and
save detected
  detected = matrix( NA, nrow = nrow(camwalk) , ncol = num.monkey.grps)
# make empty matrix save detections from obs
  perpendicular = vector()
  transect.num = vector()

  #Starting position of monkeys; x and y = sample from a uniform
distribution (runif) from 0 (min) to grid.size (max)
  monkeys.pos = cbind( x = runif(num.monkey.grps, 0,grid.size.x),
                       y = runif(num.monkey.grps, 0,grid.size.y))
 }
```

```
# loop
  for ( i in 1: nrow ( camwalk ) ){
    #i=552

    # cami's position
    cam.pos = camwalk[i,]

    # distance to each monkey
    mcd = mon.cam.dist( cam.pos,monkeys.pos)

    # does monkey detect cam
    monkdetects = monk.detect.funct(mcd, monk.scale.param =
monk.scale.param,monk.shape.param = monk.shape.param)

    # is monkey detected by cam
    detected = c( detect.funct(mcd,scale.param = scale.param,shape.param =
shape.param) )

    #  perpendicular distance to transect. the ones in matrix detected that are
= 1,
    #  calculate perpendicular distance and store in perpendicular matrix
    whi =  which( detected == 1)
    # # # # # work
    # if ( length ( whi ) > 0 ){
    #   stop ( )
    # }
    # # # # # #
    perp = perp.funct( camwalk[i,] , monkeys.pos )
    if ( length (whi) > 0 ){
      perpendicular = c( perpendicular , perp[whi])
      transect.num = c( transect.num , rep ( ceiling( i/numsteps) ,length(whi) ))
    }

    # move the monkeys!
    monkeys.pos.list = get_monkeys_pos( monkeys.pos = monkeys.pos,
                                cam.pos = cam.pos,
                                speed.dist.rate.decay = speed.dist.rate.decay,
                                grid.size.x = grid.size.x,
                                grid.size.y = grid.size.y,
                                kappa = kappa,
                                monkdetects = monkdetects,
```

```
                        mcd = mcd,
                        fid.param = fid.param,
                        norm.mean=norm.mean)
  dx = monkeys.pos.list[[2]]
  dy = monkeys.pos.list[[3]]
  monkeys.pos = monkeys.pos.list[[1]]

  # Remove monkeys once spotted
  monkeys.pos[whi,] = NA
  monkeys.pos = monkeys.pos[which ( complete.cases(monkeys.pos)),]
  #print(nrow( monkeys.pos))

  # plot
  if( plot_monk) {
   plot.grid.monk(cam.pos,
            monkeys.pos,
            cam.rad,
            detected.4.plot =  detected,
            monkeydetects = monkdetects,
            i = i, grid.size.x = grid.size.x, grid.size.y =  grid.size.y)
  }
 }

 # Video
 if( plot_video_slides){
  dev.off() # sometimes needs to be run twice
 }

 # Make a dataframe of encounters and perpendicular distances
 # All units need to be the same (i.e. all m or all km)

 dat = data.frame ( distance = as.numeric(as.vector( perpendicular))/1000,
# converting distances to km
            Area = (grid.size.x/1000) * (grid.size.y/1000),  # size of the region
of interest (for density estimate) in km
            Region.Label = "Gola",  # Stratum containing the transect (in this
case all in the same region)
            Effort =  ((grid.size.y/1000)-5) , #Lenght of transects (depends on
size of grid)
            Sample.Label = transect.num)  #  ID of the transect (repeat from
1 to however many transects)
```

```
# Give dataframe with complete cases (i.e. remove all NAs)
 dat = dat[complete.cases(dat),]

 # Add the transects that are not present in Sample.Label (i.e. the ones with
no detections) to dat dataset to account for effort
 whi = which( ! 1:numtransects %in% unique(dat$Sample.Label) )
 for ( i in whi){
  dat = rbind(dat , c( distance = NA,
                Area = (grid.size.x/1000) * (grid.size.y/1000),
                Region.Label = "Gola",
                Effort =  ((grid.size.y/1000)-5) ,
                Sample.Label = i))
 }
 # fix dataset for bug which happens when there are no detections
 if( !any( !is.na(dat[,1] ))){
  dat = as.data.frame(cbind( distance = NA,
                    Area = (grid.size.x/1000) * (grid.size.y/1000),
                    Region.Label = "Gola",
                    Effort =   ((grid.size.y/1000)-5) ,
                    Sample.Label = 1:numtransects))
 }

 # return
 return(dat)

}
```

 # Run model under chosen scenarios

```
# running the model under different scenarios

{# skip to loop

 # housekeeping
 rm(list=ls())

 # libraries
 library(monkeyMAD)
 library(circular)
 library(Distance)
```

```
 #Data
 load(file.path(PROJHOME, "Data", "EmpiricalData.rda"))

 # Scenarios:

 # Location specific

 # GRNP vs CF (FID, monkey detection, density)

 # monkey detection functions
# objects - unchangable
 scale.shape = cbind(c(25,38,41),c(2,3,3),c("detlowhunt",
"dethighhuntdiana","dethighhuntspot"))

 # objects - changable
 n.iter = 100
 grid.size.x = 147500
 num.transects = 60


# variables
 monkey.detection = c("detlowhunt", "dethighhuntdiana",
"dethighhuntspot")  # how good is the monkey at detecting observer (2
detection functions)
 region = c("FIDhighhunt", "FIDlowhunt") # I.e. community forest and GRNP
- FID
 density = c(2.5,4)  #  Different densities of monkeys based on literature
hunting intensity
 species = c("Diana", "Spot")  # Diana and spot-nosed
 n.steps = c( 40, 80, 160)  # number of steps per transect
 flee.mean = c(30, 60, 120)  # mean of the normal distribution for monkey
fleeing
 plot.detect = T

 # dataframe
 vars = expand.grid(monkey.detection,density,region,species,n.steps,
flee.mean, stringsAsFactors = F)  # Create a data frame from all
combinations of factor variables
 names(vars) =
c("monkey.detection.function","density","region","FID","num.steps","flee.
mean")  # Name the variables columns
```

```
 # remove rows
 v1= which ( vars$FID == "Diana" & vars$monkey.detection.function ==
"dethighhuntspot")
 v2= which ( vars$FID == "Spot"  & vars$monkey.detection.function ==
"dethighhuntdiana")
 vars = vars[ -c(v1,v2),]
 rownames(vars) = 1:nrow(vars)
 vars = vars[c(18,21,50,53,65:80,82,85,114,117),]
 rownames(vars) = 1:nrow(vars)

 vars2 = vars
 for ( i in 1:nrow( vars)){
  if( vars2[i,2] == 2.5){
   vars2[i,2] = "2point5"
  }
 }

 # Time (how long does it take to run)
 t1 = Sys.time()

}

# empty dataframe
varnames = c( "monkey.detection.function", "density", "region", "FID",
"num.steps", "flee.mean","density.est" , "lcl" , "ucl",
"se","sample.truncation", "sample.size" )
df = data.frame ( matrix( NA, 0, length(varnames ), dimnames = list(NULL,
varnames)))


################################################################

######################### LOOP ###############################

################################################################

par ( mfrow = c(3,4))

for( j in 1:n.iter){ # - FOR EACH ITERATION
 for ( i in 1:nrow(vars)){ # For each unique set of variables
  #i=1
```

```
  # Monkey detection
  ss = as.numeric(scale.shape[scale.shape[,3] == vars$monkey.detection.function[i],1:2])
  scale = ss[1]
  shape = ss[2]

  # Species
  whi = which(empiricalFID$Species == vars$FID[i])
  d = empiricalFID[whi,]

  # Region
  if( vars$region[i] == "highhunt"){
   d = d[d$Area == "CF",]
  }
  if( vars$region[i] == "lowhunt"){
   d = d[d$Area == "GRNP",]
  }

  # FID
  FID = d$FID

  # density
  dens = vars$density[i]

  # numsteps
  n.steps = vars$num.steps[i]

  # fleemean
  flee.mean = vars$flee.mean[i]

  # function
  namdat = c("distance" , "Area" , "Region.Label", "Effort", "Sample.Label")


  ######### Simulation

  ### RUN THE MODEL
  dat = try(suppressWarnings( model (
   monk_density_grp_km_2 = as.numeric( dens), # change only these variables
```

```
  fid.param = FID,
  grid.size.x = grid.size.x,
  numtransects = num.transects,
  numsteps = n.steps,
  monk.scale.param = scale,
  monk.shape.param = shape,
  norm.mean = flee.mean
 )))


 ####### DETECTION FUNCTION ######
 dat$distance = as.numeric(dat$distance)
 dat$distance.raw = dat$distance
 # dat$distance = as.numeric( dat$distance.raw )/1000
 dat$Area = as.numeric(dat$Area)
 dat$Effort = as.numeric(dat$Effort)
 dat$Sample.Label = as.character( dat$Sample.Label)
 dat$Region.Label = as.character( dat$Region.Label)


 # Fitting the detection function with truncation at 100 metres
 ds1 <- try(ds(dat , truncation = 0.10))
 if ( class( ds1) == "try-error"){
  est = NA
  lcl = NA
  ucl = NA
  se = NA
  sample.truncation = NA
  sample.size = length( na.omit ( dat$distance))
 } else {
  d2 = summary(ds1)
  est =  d2$dht$individuals$D$Estimate # location of density estimate in
summary output
  # location of density estimate confidence limits
  lcl =  d2$dht$individuals$D$lcl
  ucl =  d2$dht$individuals$D$ucl
  # location of density estimate standard error
  se = d2$dht$individuals$D$se
  sample.truncation = d2$dht$individuals$summary$n
  sample.size = length( na.omit ( dat$distance))
 }
```

```
# plot detection function?
   if ( plot.detect){
    try(plot(ds1, main = paste( vars[i,], collapse = "")))
   }

   ##### SAVE THE DATAFRAME
   t2 = Sys.time()
   print(t2- t1)
   t1 = t2 # Time estimate for each iteration
   print( paste( "Variables row = " , i , "--- Iteration = " , j )) # take stock
   t3 = gsub( " " , "_", t2)
   t4 = gsub( ":" , "-", t3)

   fileName = paste( c( as.character(vars2[i,]), t4,  "rda"),collapse = ".")
   save( dat , file = file.path(PROJHOME,"Output","Detection_data",fileName))

   # save to ourputmatrix
   vec.final = data.frame ( as.vector ( c( vars[i,], est, lcl, ucl, se, sample.truncation, sample.size )))
   names( vec.final ) = varnames
   df = rbind (df, vec.final)
   print( tail(df))
  }
}
```

 # Results

```
# processing model outputs
#  extracting density estimates, analysing them in distance package

# housekeeping
rm(list = ls())

# library
library(Distance)


###  ESTIMATE DENSITY
```

```
# files/folders
fold = file.path(PROJHOME , "Output", "Detection_data")
files = list.files(fold)
# split file names
spl = as.data.frame( stringr::str_split_fixed(files,"\\.",8 )[,1:5])
spl = as.data.frame ( spl)
whi = which (spl[,2] == "2point5" )
spl$V2 = as.character(spl$V2)
spl$V2[whi] =  "2.5"
names( spl) = c( "detection" , "density" , "FID" , "Species", "num.steps")

spl$est = NA
spl$lcl        = NA
spl$ucl        = NA
spl$se         = NA
spl$sample.size = NA

par (mfrow = c(3,4))

# loop
for ( i in 1:length(files)){
 #i=2

 # data
 load( file.path(fold, files[i]))

 # calculate detection function from distances and density estimate (if area
is provided)
 dat$distance = as.numeric(dat$distance)
 dat$Area = as.numeric(dat$Area)
 dat$Effort = as.numeric(dat$Effort)
 #dat$Sample.Label = 1:nrow(dat)
 #hist (dat$distance , xlim = c(0,0.1) , breaks = 3000)

 # Fitting the detection function with truncation at 100 metres
 ds1 <- try( ds(dat,truncation = 0.1))
 try ( plot ( ds1 , main = paste( vars[i,], collapse = "") ))

 if ( class( ds1) == "try-error"){
  stop()
 }
```

```
  # save est
  d2 = summary(ds1)
  spl$est[i] =  d2$dht$individuals$D$Estimate
  spl$lcl       [i] =  d2$dht$individuals$D$lcl
  spl$ucl       [i] =  d2$dht$individuals$D$ucl
  spl$se        [i] =  d2$dht$individuals$D$se
  spl$sample.size[i] =  length( na.omit ( dat$distance))

  # takestock
  print( paste ( i , "/" , length(files)))
}

df = spl
save( df, file=
      file.path ( PROJHOME ,
 "Output" , "Density-estimates",
 paste0 ("density-estimates",
       substr( Sys.time(), 1,10) , ".rda")))
```

 # code for the different functions

 # camwalk.funct

```
# This function gives the position of the observer at each time step
# input = number of steps (camwalk.speed)
# output = matrix of positions

camwalk.funct = function ( numsteps, numtransects, grid.size.x, grid.size.y,
dy = 2500){

  # objects
  # numsteps = 320
  # numtransects = 2
  # grid.size.x = 27500
  # grid.size.y = 9000
  # dy = 2500
```

```
 xvar = seq( 0, grid.size.x, length.out = numtransects+2)[2:(numtransects+1)]
 dx = diff( xvar)[1]

 camwalk = cbind( x = rep( xvar, each =  numsteps),
            y = rep( seq( dy , (grid.size.y- dy ),length.out = numsteps),numtransects))
 return(camwalk)
}
```

 # plot.grid.monk

```
 # This function plots the grid, the observer and the monkeys and writes DETECTED if any == 1 input = position of observer and monkeys, radius around observer, size of the grid and whether any detected
 # output = plot with observer as black dot and monkeys as red dots


plot.grid.monk = function ( cam , monks , cam.radius , grid.size.x = 100 ,
                  grid.size.y= 100, detected.4.plot, monkeydetects, i = NULL) {

 # objects
 # cam = camwalk[i,]
 # monks = monkeys.pos
 # cam.radius = cam.rad
 # grid.size = 100
 # detected.4.plot = detected[i,]
 # monkeydetects = monkdetects

 # vars
 g10 = (grid.size.x/10)
 #plot empty grid
 plot( 1,2 , type = "n",
     ylim = c(0,grid.size.y),
     xlim = c(0,grid.size.x),
     ylab = "y", xlab = "x", main = i)

 #add points
 points( cam[1],cam[2], pch= 19)
 points( monks , col = "brown")
 #plotrix::draw.circle( cam[1] , cam[2] , cam.rad)
```

```
 if( any( na.omit(  detected.4.plot ) == 1)){
  legend( g10,g10, legend =    "cami saw a monkey!!" , bty = "n",
text.col="blue")
 }

 if( any( monkeydetects == 1)){
  legend ( (grid.size.x-g10),g10, legend = "SEEN!", bty = "n", text.col="red")
 }

}
```

 # mon.cam.dist

```
# This function calculates the distance between the observer and the
monkeys at each time step
# input = positions of observer and monkeys
# output = distances between observer and all monkeys

mon.cam.dist = function (cam , monks){

 # VARIABLES
 # cam = camwalk[i,]
 # monks = monkeys.pos

 # OBJECTS
 num.monkeys = ifelse ( is.null(nrow(monks)),1,nrow(monks))

 # DISTANCE
 #make an empty vector called dist. rep is repeating values in x (in this case
NA for empty vector) for number of monkeys
 #empty vector will be filled by the function return
 dist = rep(NA, num.monkeys)

 # at each position of observer (X) and monkeys (Y), calculate the sides as
difference between x and y positions
 # and then the hypothenuse (i.e. distance between observer and monkey)
 for ( i in 1:num.monkeys){

  X = cam        #camwalk
  if( num.monkeys == 1){ # monkeys
```

```
    Y = monks
    } else {
     Y = monks[i,]
    }
  c =  abs( X[1] - Y[1] ) # distance
  d =  abs( X[2] - Y[2] )
  e = sqrt( c^2 + d^2 )

  dist[i] = e
 }

 # return distance
 return( dist )

}
```

 # perp.funct

```
# This function calculates the perp distance from monkey to the line given distance of monkey from cami
# input = observer position at each time step, monkey position, distance between them

perp.funct = function(cam,monks){

 #objects
 # cam = camwalk[i,]
 # monks = monkeys.pos

 perp.dist = rep(NA, nrow(monks))

 # at each position of observer (X) and monkeys (Y), with distance (mcd), calculate the perp distance
 #between monkey and transect
 for ( i in 1:nrow(monks)){
#i=28
  X = cam        #camwalk
  Y = monks[i,]   #monkey.pos
  a =  abs( X[1] - Y[1] )
```

```
  perp.dist[i] = a
 }

 # return distance
 return( perp.dist )
 }
```

 # monk.detect.funct

```
# This function specifies whether monkeys detect me or not
# input= distance between cami and monkey, model specifications (curve - probability of detection at different distances)
# output= whether detected or not (and thus following on from this whether they run away or not)

monk.detect.funct = function( mcd, monk.scale.param, monk.shape.param){

 # objects

 # mcd = mcd
 # monk.model = NULL
 # detection.rate = detection.rate
 # max.det.distance = max.det.distance
 # monk.scale.param = monk.scale.param
 # monk.shape.param = monk.shape.param


 # hazard rate model = underlying model for the detection process
  y = 1 -exp(-(mcd/monk.scale.param)^-monk.shape.param)

 #does the monkey detect the observer?

 monk.detect = rbinom( length(mcd), 1,y)

 #return
 return(monk.detect)

}
```

 # detect.funct

```
# This function specifies whether monkeys is detected or not
# input= distance between cami and monkey, model specifications (curve - probability of detection at different distances)
# output= whether detected or not

detect.funct = function( mcd, scale.param, shape.param){

 # objects

 # hazard rate model = underlying model for the detection process
 y = 1 -exp(-(mcd/scale.param)^-shape.param)

 #is the monkey detected?
 detect = rbinom( length(mcd), 1,y)

 #return
 return(detect)

}
```

 # get_monkey_pos

```
# This function gives the movement of the monkeys at each time step
# Direction of movement depends on whether monkeys detects observer and whether they are close enough (FID) to flee
# input = monkey starting position, monkey speed, grid size, direction of movement(mu), narrowness of bell (kappa)
# output = monkey new position at each time step

get_monkeys_pos = function (monkeys.pos, cam.pos, speed.dist.rate.decay, grid.size.x, grid.size.y, kappa, monkdetects, mcd, fid.param, norm.mean=60){

 # objects

 # monkeys.pos = monkeys.pos
 # cam.pos = cam.pos
 # speed.dist.rate.decay = speed.dist.rate.decay
 # grid.size.x = grid.size.x
```

```
# grid.size.y = grid.size.y
# kappa = kappa # default for no
# monkdetects = monkdetects
# mcd = mcd
# fid.param = fid.param
# pois.const = 10

# libraries
library(circular)

#add in monkey direction and new position
num.monkeys = nrow(monkeys.pos)

# empty objects
dx = rep(NA,num.monkeys)
dy = rep(NA,num.monkeys)

for (j in 1:num.monkeys){
 #{
 # j=1

 # direction to cam
 mu = get_heading(cam.pos[1],
            cam.pos[2],
            monkeys.pos[j,1],
            monkeys.pos[j,2])


 ######## If monkey detects cami, MOVE AWAY

 # fid
 sampled.fid = sample(fid.param,1)

 if (monkdetects[j] == 1 & mcd[j] < sampled.fid ){

  monkey.dir = rvonmises (1,circular(mu), kappa, control.circular=list(units="radians")) #vonmises distribution
  monkey.dir = ifelse (monkey.dir > pi,monkey.dir -2*pi, monkey.dir)
  monk.speeds = rnorm (1, mean=norm.mean, sd=10) # normal distribution for fleeing speed
```

```
    } else {

     ###### otherwise RANDOM WALK

     monkey.dir  = runif(1, -pi , pi) # runif distribution
     monk.speeds  =  round  (  rexp(  1,  speed.dist.rate.decay))  #exponetial
decay curve

   }

   if ( monkey.dir  > -pi && monkey.dir < (-pi/2)){
    theta = pi +
      monkey.dir
    dx[j] = -abs( monk.speeds * sin(theta) )  # change in x
    dy[j] = -abs( monk.speeds * cos(theta) )  # change in y
   }
   if ( monkey.dir  > (-pi/2) && monkey.dir < 0){
    theta = -pi/2 +
      monkey.dir
    dx[j] = -abs( monk.speeds * cos(theta) )
    dy[j] = abs( monk.speeds * sin(theta) )
   }
   if ( monkey.dir > 0 && monkey.dir < (pi*(1/2)) ){
    theta = 0 +
      monkey.dir
    dx[j] = abs( monk.speeds  * sin(theta) )
    dy[j] = abs( monk.speeds * cos(theta) )
   }
   if ( monkey.dir > (pi*(1/2)) && monkey.dir < (pi) ){
    theta = pi*(1/2) +
      monkey.dir
    dx[j] = abs(monk.speeds  * cos(theta) )
    dy[j] = - abs(monk.speeds * sin(theta) )
   }
   monkeys.pos[j,] = monkeys.pos[j,] + c(dx[j],dy[j])
  }

  for ( j in 1:2){
   #j=2

   if ( j == 1){
```

```
    grid.size = grid.size.x
   }
   if ( j == 2){
    grid.size = grid.size.y
   }
   monkeys.pos[,j] =ifelse ( monkeys.pos[,j] > grid.size,grid.size,
monkeys.pos[,j] ) # if any monkey position (x and y- i.e. columns) above
100,let it be = 100
   monkeys.pos[,j] =ifelse ( monkeys.pos[,j] < 0      , 0,      monkeys.pos[,j] )
# if any monkey position (x and y- i.e. columns) below 0, let it be = 0
  }

  monkeys.pos = cbind(monkeys.pos)

  return(list ( monkeys.pos, dx,dy))
}
```

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